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HABITAT ASSOCIATIONS FOR EASTERN BLACK RAIL (*Laterallus jamaicensis jamaicensis*) IN SOUTH FLORIDA

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Abstract.—Identification of important habitat features can help facilitate recovery for threatened and endangered species, but this information is not always readily available prior to implementing management actions. The Eastern Black Rail (*Laterallus jamaicensis jamaicensis*) was recently listed as federally threatened and management efforts are shifting toward inland locales in lieu of the coastal areas where the species was historically found to avoid the effects of ongoing sea level rise. Little is known about inland Eastern Black Rail populations, so we examined habitat parameters that were important to predicting occupancy of the South Florida Everglades population. We found that saturated soils, topographic heterogeneity, and herbaceous cover had a positive effect on occupancy and the number of trees was negatively associated with occupancy. We also found that extinction rates were higher for locations that dried between years. While hydrology and herbaceous cover are known to influence Black Rail occupancy for coastal Eastern Black Rails and inland California Black Rails (*L. jamaicensis coturniculus*), the effect of topographic heterogeneity is novel and represents a potential feature that land managers can manipulate to increase inland habitat suitability for the Eastern Black Rail.

Key words: Black Rail, endangered species, Everglades, habitat management, hydrology, *Laterallus jamaicensis*

Identifying habitat features that are important to threatened and endangered species is crucial to managing habitat that facilitates recovery, but this information is not always readily available. Information may be deficient because these species are inherently rare (Hernandez et al. 2006), the species is secretive and difficult to detect (Eddleman et al. 1988, Conway and Gibbs 2005), or the species' historical habitat has disappeared or is no longer viable (Gregory et al. 2013). When faced with deficient information about endangered and threatened species,

land managers may base management decisions on studies of closely related species (Parlato and Armstrong 2018, Doll et al. 2022) and expert opinion (McCleery et al. 2007) but both strategies can result in ineffective actions (Regan et al. 2004, Henry et al. 2019). Exploratory field studies should be conducted, if possible, to overcome data deficiency for at-risk species (Bland et al. 2017, Hochkirk et al. 2021).

The Black Rail (*Laterallus jamaicensis*) is a small secretive bird found patchily in freshwater and tidally influenced wetlands (Watts 2016). The nominate subspecies, Eastern Black Rail (*L. jamaicensis jamaicensis*), is listed as threatened under the Endangered Species Act (U.S. Fish and Wildlife Service 2020). Historically, this form primarily occurred in salt marshes along the Atlantic Coast and population declines are believed to be related to increased coastal flooding associated with sea level rise (Watts 2016, Watts et al. 2021). Given the expected continued increase in coastal flooding (Vitousek et al. 2017), managers have begun to prioritize conservation beyond the reach of tidal influence (Atlantic Coast Joint Venture 2020) but lack data supporting management actions in inland settings.

Because there have been few studies of Eastern Black Rails in non-tidal habitats, it is unclear how habitat should be managed. Studies of the closely related California Black Rail (*L. j. coturniculus*) have shown that occupied inland habitats most often provide water at 1–3-cm depths, dense vegetation, and relatively stable hydrology throughout the summer breeding season (Flores and Edelman 1991, Richmond et al. 2010). Most inland California Black Rails are found in wetlands where water is sourced through direct irrigation or leaks in irrigation infrastructure, both of which can lead to a stable hydrologic regime (Richmond et al. 2008, 2010). Without irrigation, wetlands within this landscape tend to dry out during the hot and dry summer months (Lewis et al. 2000).

Unlike California Black Rail habitats, precipitation is greatest during the summer along the eastern United States so Eastern Black Rails must cope with water levels that can rise as the summer breeding season progresses (Prat and Nelson 2014, Watts 2021). The landscapes that Eastern Black Rails occupy are much flatter than inland California Black Rail habitats. A flatter landscape is associated with slower rainwater drainage and a greater threat of flooding following heavy rainfall events, as is the case in South Carolina where coastal impoundments have been colonized (Hand et al. 2019, 2021). Topographic highs embedded within or adjacent to wetlands may mitigate this threat by providing refugia during flood events (Hand et al. 2021). Examples include occupied areas in Texas salty prairie where pimple mounds offer refugia from high water (Haverland 2019), wetlands that are more likely to be occupied when adjacent to higher elevation forests in South Carolina (Roach and Barret 2015),

and occupied wetlands that include areas of relatively high and low elevation at St. Johns National Wildlife Refuge in eastern Florida (M. L. LeGare, Merritt Island National Wildlife Refuge, pers. comm.).

We surveyed non-tidal settings in South Florida to understand how topographic diversity and other habitat characteristics contribute to Eastern Black Rail occupancy. Understanding how topography relates to Eastern Black Rail occupancy would benefit habitat management by identifying areas that provide ideal topographic relief but lack other important characteristics of Black Rail habitat that could be otherwise improved and providing guidance on managing topography at locations where suitable water supply and herbaceous cover are already available.

METHODS

Study area.—We conducted our study at Big Cypress National Preserve, Everglades National Park, and the Southern Glades Wildlife Environmental Area (Fig. 1) which are all part of the Everglades, the largest subtropical wetland in the United States (Richardson 2010). Land cover types include graminoid prairies, mangroves swamps, and forested tree islands (Davis and Ogden 1994) and are a result of the underlying geology,

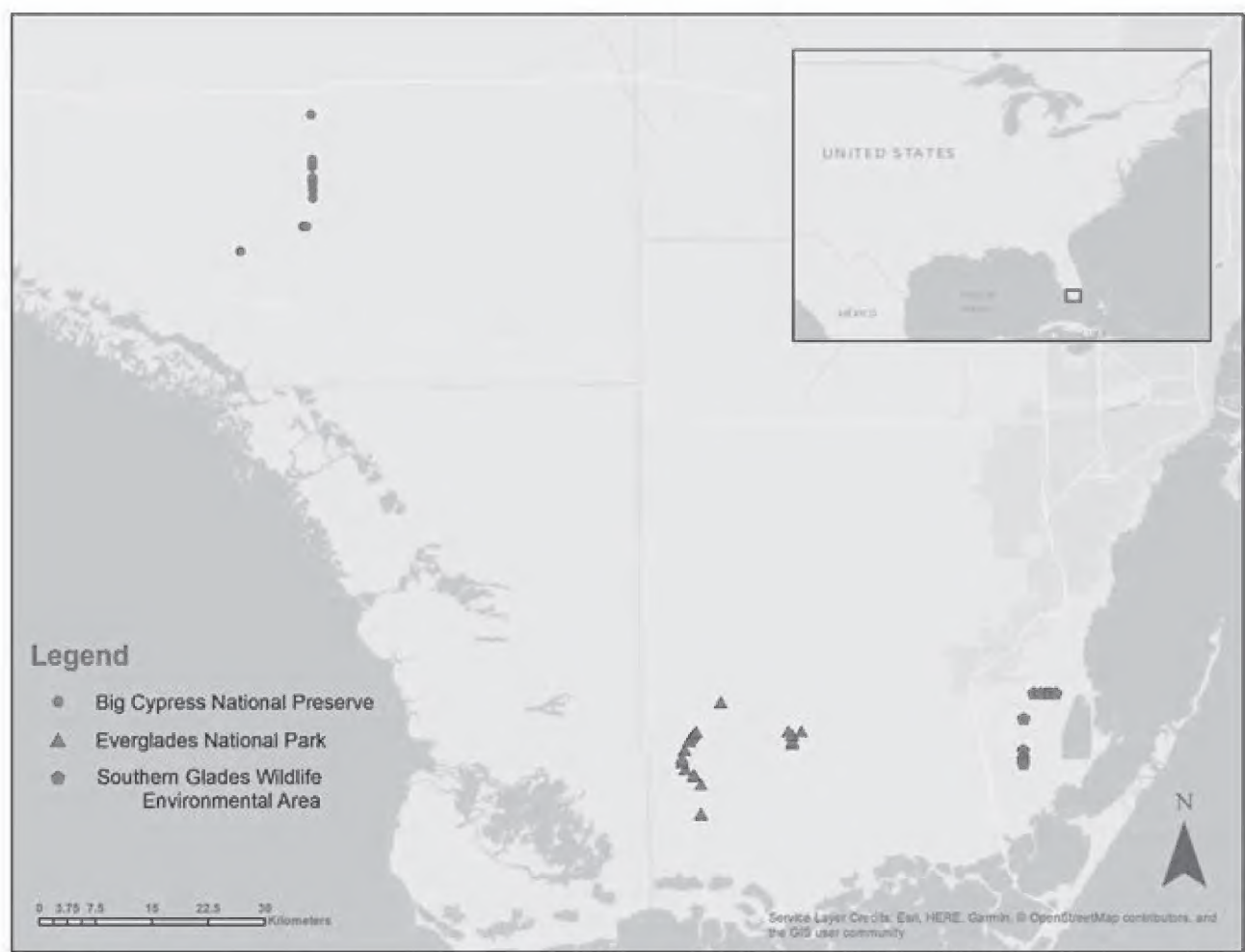


Figure 1. Study area for Eastern Black Rail surveys in South Florida during 2020–2021.

fire frequency, and length of time that habitat is inundated (i.e., hydroperiod) following seasonal rains that typically last from June–October.

Black Rail surveys.—We surveyed Black Rails during 19–24 February 2020 and 07–22 March 2021 during mornings from one hour before sunrise to three hours after sunrise and evenings from three hours before sunset to one hour after sunset. Our point count network included 12 survey points at Big Cypress National Preserve, 19 points at Everglades National Park, and 9 points at Southern Glades Wildlife Environmental Area. We selected 18 points where black rails had been detected in past efforts and 22 randomly selected points where black rails were not observed in those efforts. We conducted three rounds of point counts at 37 locations, two rounds at one location, and one round at two locations during 2020. We conducted three rounds of point counts at all 40 locations during 2021. We conducted surveys from the margins of public roads and survey points were ≥ 400 m apart. We set FoxPro game callers (FoxPro, Lewistown, PA, USA) to 70–80 db and broadcast a 10-minute survey track that included Black Rail vocalizations alternating with silent listening periods. Vocalizations used included a combination of ki-ki-kerr, churt, growl and eek-eek calls.

Habitat characteristics.—During the 2021 field season, we quantified topography, vegetation, and hydrology at 25 habitat survey locations spaced 30 m apart in a 1.44-ha square polygon approximately 25 m away from the roads where black rail point count surveys were conducted. We chose the size of this plot because it was near 95% minimum convex polygon home range sizes for Black Rails reported in eastern Florida (0.98 ha; LeGare and Eddleman 2001), Louisiana (0.71 ha; Johnson and Lehman 2021), and Texas Florida (0.62 ha for females, 1.3 ha for males; Haverland et al. 2021). We conducted habitat surveys on the same day as a point count survey or one day later.

We measured relative elevation with a tripod, transit level, and measurement rod (Dorf 2018). The tripod and level were near the center of the plot with an unobstructed view of other points. One biologist operated the level and the other biologist visited the 25 habitat survey locations within the plot and held the measurement rod. We used these measurements to calculate three measures of topographic diversity (Shepard et al. 2001) including topographic range (greatest elevation – lowest elevation), surface roughness (arithmetical mean deviation of elevations), and root-squared surface roughness (root mean squared deviation of elevations).

We visually estimated percent ground cover (tree, shrub, grass, open water) within the perimeter of the habitat survey plot and counted all trees and shrubs taller than 2 m within the plot. At each habitat survey location, we also counted the number of plant stems that touched each 10-cm section of a Wiens pole (Wiens 1969). At a subset of five habitat survey locations at each plot, we identified and estimated cover (to nearest 5%) of all plant species within a 0.25-m² plot and identified to species (if possible) all stems that touched each 10-cm section of the Wiens pole.

We visually assessed hydrology as standing, saturated, damp, or dry at each habitat survey point. If standing water was present, we measured the water depth with a Wiens pole to the nearest cm and considered water to be shallow if depth was ≤ 3 cm. We determined whether the points were wetter (greater water depth) or drier (lower water depth) in 2021 than when we conducted Black Rail surveys in 2020 using the nearest Everglades Depth Estimation Network (<https://sofia.usgs.gov/eden/index.php>) water gauge to each survey point.

Statistical analysis.—We quantified Black Rail occupancy in South Florida using dynamic occupancy models, which estimate occupancy, colonization, extinction, and detection rate when detection is imperfect (Mackenzie et al. 2003). We performed our analyses in a Bayesian framework, which can better estimate parameters for studies with low sample sizes (Lee and Song 2004), with package *ubms* (Kellner et al. 2021) in Program R (R Core Team 2021). We used a multi-step process to select the best model using the expected log predictive density (ELPD) calculated with leave-one-out cross-validation information criterion (LOOIC; Vehtari et al. 2017). At each step, we compared models that includ-

ed predictors to a null model to determine if and which predictors should be included in subsequent steps. Our first step included evaluating whether including observer or background noise in the detection function improved model fit while holding all other functions (initial occupancy, extinction, and colonization) constant. All downstream models included the best fitting predictors in the detection function. We then selected the best predictors to include within the occupancy function by holding the extinction and colonization functions constant and comparing all potential hydrology (number of points that were inundated, shallow water [≤ 3 cm standing water], or saturated soil), patch-level vegetation (number of trees > 5 cm diameter at breast height [DBH], number of shrubs > 1 m tall, overall percent shrub cover, overall percent tree cover, and combined percent shrub and tree cover), point-level vegetation, and topography (topographic range [greatest elevation – lowest elevation], surface roughness [arithmetical mean deviation of elevations], root-squared surface roughness [root mean squared deviation of elevations]) predictors individually. Annual changes in hydrology may have influenced extinction and colonization of sites so we also compared models that included a coarse measure of hydrological change from 2020 to 2021 (wetter or drier as measured by the nearest water gauge to each study site) in the extinction and colonization functions while holding the occupancy function constant. We then constructed a model using the best-fitting hydrology, patch-level vegetation, point-level vegetation, and topography predictors. For predictors that were < 4 ELPD points from the top predictor within the same category (hydrology, patch-level vegetation, point-level vegetation, topography), we compared final models that included each (Sivula et al. 2022). We scaled and centered all continuous predictors. We used four Markov chain Monte Carlo chains with 2,000 iterations, including 1,000 warm-up iterations. We used 100 draws for posterior predictions and report 95% uncertainty intervals (UI) for effect sizes and predictions. We also compare and report mean herbaceous cover, mean tallest height that plants touched the Wiens pole, dominant plant species (species with highest percent cover), percentage of points with saturated water and percentage of points with shallow water (≤ 3 cm) at survey plots that were occupied and unoccupied for comparison to other studies.

RESULTS

Occupancy.— During 2020 and 2021, we recorded Black Rail observations at 20 of 40 locations including 18 points in 2020. We only recorded Black Rails at 7 of 20 locations in 2021 including five locations where Black Rails were observed in 2020 and two locations where Black Rails were unobserved during 2020. Our top Black Rail occupancy model included surface roughness derived from survey-level measurements, the number of saturated points, the number of trees on plot with a DBH > 5 cm, and mean point-level herbaceous vegetation cover within the occupancy function, hydrology change in the extinction function, and background noise in the detection function (Table 1).

Between 2020 and 2021, occupancy decreased from 0.61 (95% UI = 0.58–0.68) to 0.26 (95% UI = 0.17–0.40) at our South Florida survey points. Our top model was 10.4 (± 4.18 [SE]) ELPD units better than the second highest ranking model and predicted greater occupancy on plots with more saturated soils ($\beta = 12.14$, 95% UI = 4.31–22.15; Fig. 2A), greater surface roughness ($\beta = 8.58$, 95% UI = 2.41–17.08; Fig. 2B), greater ground cover ($\beta = 6.64$, 95% UI = -0.36 –14.98; Fig. 2C), and lower occupancy at plots with more trees > 5 cm DBH ($\beta = -11.58$, 95% UI = -21.81 – -3.35 ; Fig. 2D).

Table 1. Models estimating occupancy for Eastern Black Rail in South Florida during 2020–2021. Population parameters include occupancy (ψ), colonization (γ), extinction (ξ), and detection probability (ρ). Reported statistics include (K), leave-one-out information criterion (LOOIC), expected log predictive density estimate (ELPD), difference between ELPD and the ELPD of top model (Δ ELPD), standard error for Δ ELPD (Δ ELPD SE), and LOO model weight (LOO weight).

Parameters	K	LOOIC	ELPD	Δ ELPD	Δ ELPD SE	LOO weight
ψ (saturated points + roughness + herbaceous cover + trees > 5 cm DBH), γ (.), ξ (hydrological change), ρ (background noise)	8.07	149.30	-74.65	0.00	0.00	0.29
ψ (saturated points), γ (.), ξ (.), ρ (background noise)	6.71	170.12	-85.06	-10.40	4.18	0.14
ψ (.), γ (.), ξ (hydrological change), ρ (background noise)	5.85	173.72	-86.86	-12.21	3.52	0.11
ψ (saturated to shallow water), γ (.), ξ (.), ρ (background noise)	7.43	175.32	-87.66	-13.01	4.22	0.00
ψ (herbaceous cover), γ (.), ξ (.), ρ (background noise)	6.84	178.76	-89.38	-14.73	4.21	0.09
ψ (shallow water), γ (.), ξ (.), ρ (background noise)	8.11	180.34	-90.17	-15.52	4.61	0.12
ψ (trees > 5 cm DBH), γ (.), ξ (.), ρ (background noise)	6.62	180.38	-90.19	-15.53	4.46	0.07
ψ (herbaceous height), γ (.), ξ (.), ρ (background noise)	8.37	181.94	-90.97	-16.32	4.43	0.00
ψ (.), γ (hydrological change), ξ (.), ρ (background noise)	6.65	182.26	-91.13	-16.48	4.30	0.00
ψ (.), γ (.), ξ (.), ρ (background noise)	6.19	182.38	-91.19	-16.54	4.31	0.00
ψ (roughness), γ (.), ξ (.), ρ (background noise)	7.58	182.62	-91.31	-16.66	4.17	0.00
ψ (root mean ² roughness), γ (.), ξ (.), ρ (background noise)	7.63	182.72	-91.36	-16.71	4.26	0.00
ψ (topographic range), γ (.), ξ (.), ρ (background noise)	7.23	182.74	-91.37	-16.72	4.22	0.00
ψ (tree cover), γ (.), ξ (.), ρ (background noise)	5.87	183.92	-91.96	-17.31	4.89	0.07
ψ (shrub and tree cover), γ (.), ξ (.), ρ (background noise)	6.07	183.96	-91.98	-17.33	4.96	0.10
ψ (damp soils), γ (.), ξ (.), ρ (background noise)	7.32	184.62	-92.31	-17.66	4.72	0.00
ψ (.), γ (.), ξ (.), ρ (background noise + observer)	10.12	185.30	-92.65	-17.99	4.65	0.00
ψ (.), γ (.), ξ (.), ρ (observer)	8.67	185.92	-92.96	-18.31	4.76	0.00
ψ (.), γ (.), ξ (.), ρ (.)	5.21	189.04	-94.52	-19.87	4.66	0.00

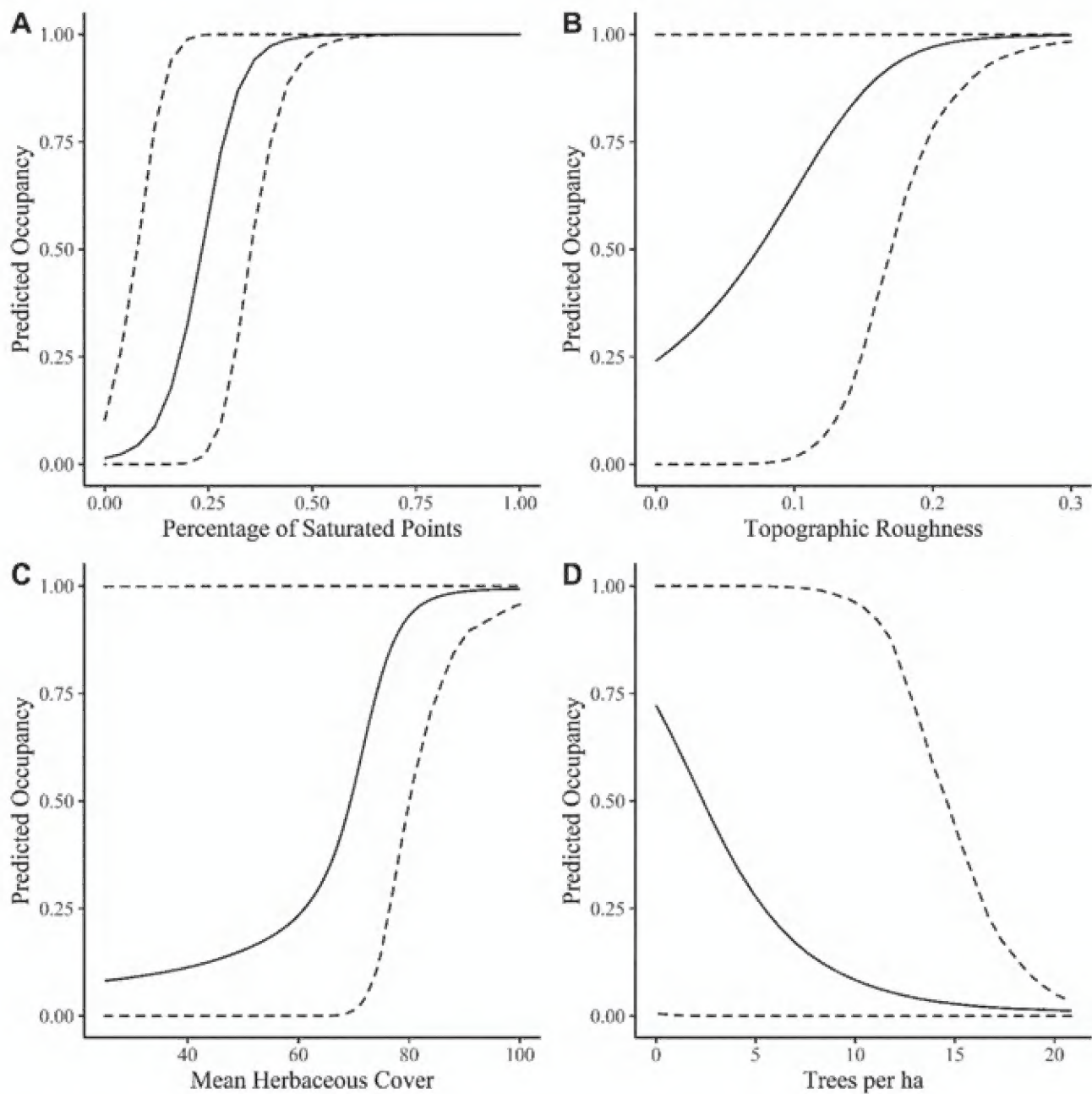


Figure 2. Influence of A) the percentage of saturated points, B) topographic roughness, C) mean herbaceous cover, and D) the number of trees on Black Rail occupancy in South Florida, 2020–2021. All predictors were held at their mean values except for the predictor of interest for each panel. Dashed lines represent 95% uncertainty intervals.

No predictors were included in the colonization function and colonization was estimated at 0.06 (95% UI = 0.00–0.24). Extinction was lower at sites that were wetter in 2021 than in 2020 ($\beta = -3.25$, 95% UI = -6.37 – 0.78). Extinction was estimated at 0.21 (95% UI = 0.01–0.59) at sites that were wetter in 2021 than they were in 2020 and at 0.79 (95% UI = 0.47–0.97) at sites that were drier in 2021 (Fig. 3). Background noise had a negative relationship with detection, though uncertainty intervals overlapped zero ($\beta = -0.12$, 95% UI = -0.56 – 0.30). The model estimated detection at 0.33 (95% UI = 0.22–0.45) at mean background noise.

Site characteristics.—Mean cover was greater at occupied locations than unoccupied locations ($t = 2.258$, $df = 19$, $P = 0.036$). The mean

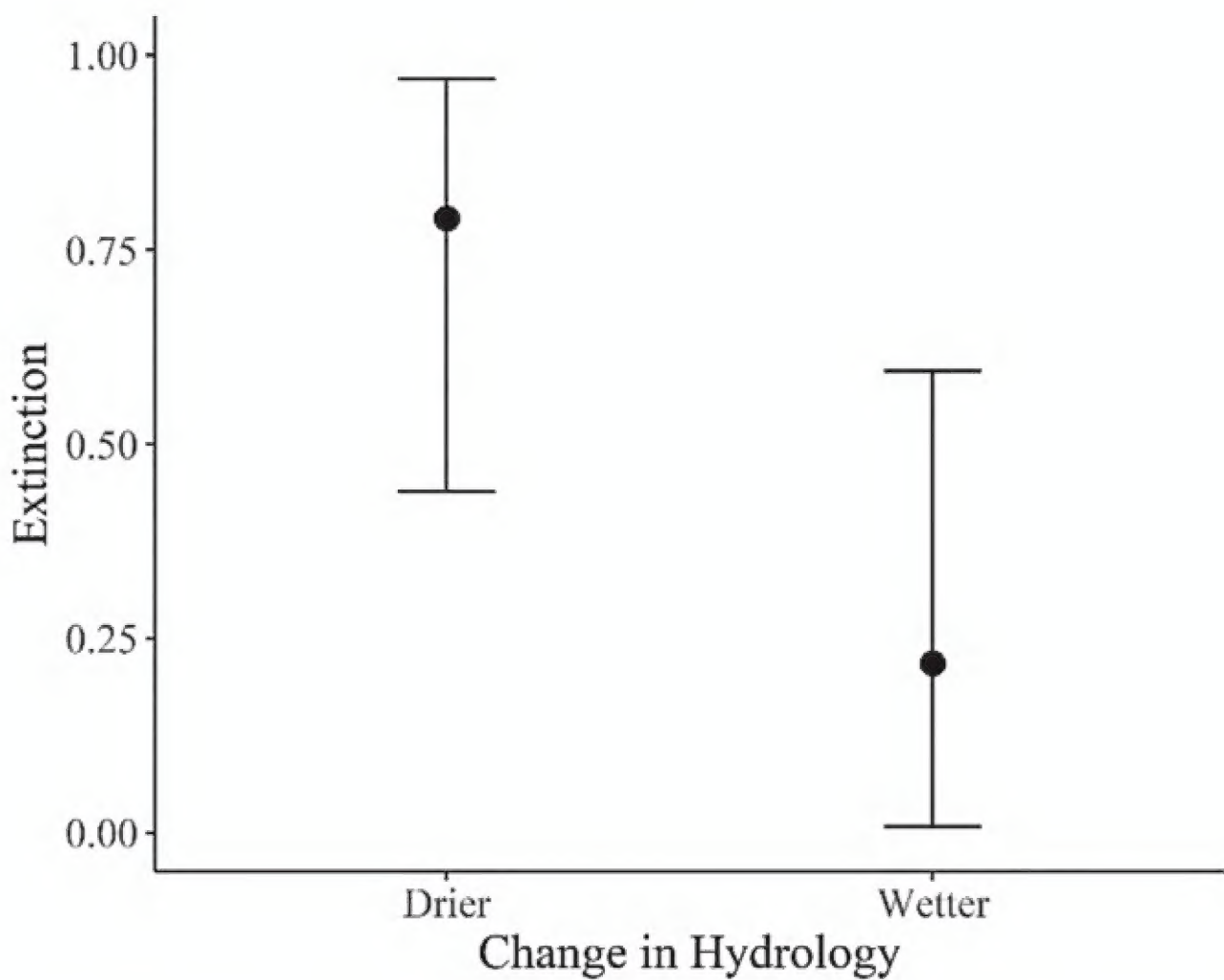


Figure 3. Influence of hydrologic change between 2020 and 2021 on Black Rail extinction in South Florida. Error bars represent 95% uncertainty intervals.

tallest plant height was not different between occupied and unoccupied locations ($t = 0.758$, $df = 19$, $P = 0.458$). The mean number of saturated points was greater at occupied sites than unoccupied ($t = 3.275$, $df = 19$, $P = 0.004$) and the mean number of points with shallow water (≤ 3 cm) was not different between occupied and unoccupied locations ($t = -0.459$, $df = 19$, $P = 0.652$; Appendix A). The plant species that was most frequently dominant at occupied survey locations was sawgrass (*Cladium jamaicense*; 12 of 20), followed by gulf hairawn muhly (*Muhlenbergia filipes*; 7) and Florida bluestem (*Andropogon floridanus*; 1). Sawgrass was also the dominant plant species at the majority of unoccupied sites (12 of 20) followed by southern beaksedge (*Rhynchospora microcarpa*; 2), black needlerush (*Juncus roemerianus*; 2), Florida bluestem (2), gulf hairawn muhly (1), and bushy bluestem (*Andropogon glomeratus*; 1).

DISCUSSION

Topographical heterogeneity, soil saturation, herbaceous cover, and tree density relate to Eastern Black Rail occupancy in South

Florida. This is especially important given the Everglades supports a relatively large inland Black Rail population and could serve as a model for inland Black Rail habitat management at other locales. Topographic diversity has not been measured in other Black Rail occupancy studies, though researchers have measured slope and alluded to topographic highs providing refuge from flooding (LeGare and Eddleman 2001, Roach and Barrett 2015, Hand et al. 2021, Haverland et al. 2021). Increasing topographic diversity through mechanical manipulation or altering hydrology and woody stem abundance in areas where the existing surface is topographically diverse may result in greater likelihood of being occupied. We found roughness values above 0.07 to be sufficient to support 50% occupancy in the South Florida landscape (Fig. 2). However, surface roughness required to support Black Rails likely varies according to characteristics unique to specific areas. For example, higher topographic highs may be required to provide refugia within a flat impoundment than the expansive Everglades where precipitation from localized thunderstorms can spread throughout the system. Within the Everglades, the benefits of topographic diversity may not be limited to providing refugia from flooding. When the Everglades dry during winter and spring, shallow water and saturated soils may persist in topographic lows while less topographically diverse (i.e., flatter) areas completely dry out. Lower topographic lows may be beneficial in other areas that regularly face drought so that shallow water and saturated soils can persist.

In addition to topography, hydrology appears to play an important role in predicting occupancy. The predictor with the strongest effect on occupancy was the mean number of points with saturated soils. California Black Rail studies have found shallow water, rather than saturated soils, to be associated with Black Rail occupancy (Flores and Edelman 1995, Richmond et al. 2010). We did not measure hydrology during the first year of our study so the parameter reflects conditions found only during 2021. Water gauges near our study sites at Everglades National Park and Southern Glades Wildlife Environmental Area measured higher water levels during 2020 survey dates than during 2021 survey dates, so these sites may have been wetter during the first survey year. Some saturated points in 2021 may have been inundated by shallow water in 2020. The between-year change in hydrology also affected extinction rates for the South Florida Black Rail population. Extinction rates were nearly four times greater for areas that were drier during the second survey year than areas that were wetter. This is consistent with dynamics of inland California Black Rails where drought can affect periodic spikes in extinction probability (Van Schmidt et al. 2019).

Vegetation also affected occupancy at our study site. The number of trees had a strong negative effect on occupancy (Fig. 2D). This is consistent with other studies of Eastern Black Rails in coastal areas, except where trees represent the only upland refugia from flooding (Hand et al. 2021). Trees within the Everglades landscape are often associated with bald cypress (*Taxodium distichum*) swamps and upland pine (*Pinus* spp.) stands. Woody plant communities such as these have displaced plant communities with species-rich herbaceous ground cover because fire is less frequent than it historically occurred (Slocum et al. 2003). Black rails in both coastal and inland settings are typically found in relatively dense herbaceous cover (Tsao et al. 2009, Richmond et al. 2010, Watts 2016). Our study also found that herbaceous cover was associated with greater occupancy (Fig. 2C), though this predictor had a smaller effect size than other predictors and 95% uncertainty intervals narrowly overlapped zero. The dominant herbaceous species were very similar among our survey locations with sawgrass being dominant at the majority of both occupied and unoccupied sites. However, the majority (7 of 8) of sites where gulf hairawn muhly was dominant supported Black Rails. Gulf hairawn muhly is a species that characterizes marl prairie (Armentano et al. 2006). Marl prairie is also characterized by shallow soil and more heterogenic topographic relief (Hanan and Ross 2010, Sah et al. 2014) so the association with Black Rail occupancy and herbaceous cover may simply be attributed to topographical diversity rather than the plant species.

If Eastern Black Rail populations continue declining as they have over the past 30 years, management actions will become more commonplace and increasingly focus on inland locations to avoid impacts associated with sea level rise. We have identified topographical, hydrological, and vegetative characteristics of occupied inland habitat within the South Florida landscape that could be used for management decisions, but continued investigation is warranted given the relatively small sample size (40 point count locations) used to derive our findings.

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LITERATURE CITED

- ATLANTIC COAST JOINT VENTURE. 2020. Eastern Black Rail Conservation Plan for the Atlantic Coast. U.S. Department of the Interior, Fish and Wildlife Service, Hadley, Massachusetts, USA. www.acjv.org, accessed 20 August 2020.
- ARMENTANO, T. V., J. P. SAH, M. S. ROSS, D. T. JONES, H. C. COOLEY, AND C. S. SMITH. 2006. Rapid responses of vegetation to hydrological changes in Taylor Slough, Everglades National Park, Florida, USA. *Hydrobiologia* 569(1):293–309.
- BLAND, L. M., J. BIELBY, S. KEARNEY, C. D. L. ORME, J. E. M. WATSON, AND B. COLLEN. 2017. Toward reassessing data-deficient species. *Conservation Biology* 31:531–539.
- CONWAY, C. J., AND J. P. GIBBS. 2005. Effectiveness of call-broadcast surveys for monitoring marsh birds. *Auk* 122:26–35.
- DAVIS, S., AND J. C. OGDEN. 1994. *The Everglades: the ecosystem and its restoration*. St Lucie Press, Delray Beach.
- DOLL, C. F., S. J. CONVERSE, AND C. B. SCHULTZ. 2022. Non-target effects of herbicides on the Zerene silverspot butterfly, a surrogate subspecies for the threatened Oregon silverspot butterfly. *Journal of Insect Conservation* 26:1–15.
- DORF, R. C. 2018. *The Engineering Handbook*. CRC Press, Boca Raton.
- HAZELTON, N. W. J., AND R. B. BUCKNER. 2018. Distance measurements. Chapter 163 in *The Engineering Handbook* (R. C. Dorf, Ed.). CRC Press, Boca Raton.
- EDDLEMAN, W., F. KNOPF, B. MEANLEY, AND F. REID. 1988. Conservation of North American rallids. *Wilson Bulletin* 100:458–475.
- FLORES, R. E., AND W. R. EDDLEMAN. 1991. Nesting biology of the California Black Rail in southwestern Arizona. *Western Birds* 24:81–88.
- GREGORY, R., J. ARVAI, AND L. R. GERBER. 2013. Structuring decisions for managing threatened and endangered species in a changing climate. *Conservation Biology* 27:1212–1221.
- HAND, C. E., W. GABEL, G. R. DIPETTO, R. E. BONAFILIA, J. M. THIBAUT, AND E. ZNIDERSIC. 2021. A window into the breeding ecology and molt of the Eastern Black Rail (*Laterallus jamaicensis jamaicensis*). *Waterbirds* 44:207–221.
- HAND, C. E., E. ZNIDERSIC, AND A. K. TEGELER. 2019. First documentation of Eastern Black Rails (*Laterallus jamaicensis jamaicensis*) breeding in South Carolina, USA in more than a century. *Waterbirds* 42:237–241.
- HANAN, E. J., AND M. S. ROSS. 2010. Across-scale patterning of plant-soil–water interactions surrounding tree islands in Southern Everglades landscapes. *Landscape Ecology* 25:463–476.
- HAVERLAND, A. A. 2019. Determining the status and distribution of the eastern Black Rail (*Laterallus jamaicensis*) in coastal Texas. Dissertation, Texas State University, San Marcos, USA.
- HAVERLAND, A. A., M. C. GREEN, F. WECKERLY, AND J. K. WILSON. 2021. Eastern Black Rail (*Laterallus jamaicensis jamaicensis*) home range and habitat use in late winter and early breeding season in Coastal Texas, USA. *Waterbirds* 44:222–233.
- HENRY, E., E. BRAMMER-ROBBINS, E. ASCHEHOUG, AND N. HADDAD. 2019. Do substitute species help or hinder endangered species management? *Biological Conservation* 232:127–130.
- HERNANDEZ, P. A., C. H. GRAHAM, L. L. MASTER, AND D. L. ALBERT. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29:773–785.
- HOCHKIRCH, A., M. J. SAMWAYS, J. GERLACH, M. BÖHM, P. WILLIAMS, P. CARDOSO, N. CUMBERLIDGE, P. J. STEPHENSON, M. B. SEDDON, V. CLAUSNITZER, AND P. A. BORGES. 2021. A strategy for the next decade to address data deficiency in neglected biodiversity. *Conservation Biology* 35:502–509.
- JOHNSON, E. I., AND J. LEHMAN. 2021. Status and habitat relationships of the Black Rail (*Laterallus jamaicensis*) in Coastal Louisiana, USA. *Waterbirds* 44:234–244.

- KELLNER, K. F., N. L. FOWLER, T. R. PETROELJE, T. M. KAUTZ, D. E. BEYER JR, AND J. L. BELANT. 2022. *ubms*: an R package for fitting hierarchical occupancy and N mixture abundance models in a Bayesian framework. *Methods in Ecology and Evolution* 13:577–584.
- LEE, S. Y., AND X. Y. SONG. 2004. Evaluation of the Bayesian and maximum likelihood approaches in analyzing structural equation models with small sample sizes. *Multivariate Behavioral Research* 39:653–686.
- LEGARE, M. L., AND W. R. EDDLEMAN. 2001. Home range size, nest-site selection and nesting success of Black Rails in Florida. *Journal of Field Ornithology* 72:170–177.
- LEWIS, D., M. J. SINGER, R. A. DAHLGREN, AND K. W. TATE. 2000. Hydrology in a California oak woodland watershed: a 17- year study. *Journal of Hydrology* 240:106–117.
- MACKENZIE, D. I., J. D. NICHOLS, J. E. HINES, M. G. KNUTSON, AND A. B. FRANKLIN. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200–2207.
- MCCLEERY, R. A., R. R. LOPEZ, AND N. J. SILVY. 2007. Transferring research to endangered species management. *Journal of Wildlife Management* 71:2134–2141.
- PARLATO, E. H., AND D. P. ARMSTRONG. 2018. Predicting reintroduction outcomes for highly vulnerable species that do not currently coexist with their key threats. *Conservation Biology* 32:1346–1355.
- PRAT, O. P., AND B. R. NELSON. 2014. Characteristics of annual, seasonal, and diurnal precipitation in the Southeastern United States derived from long-term remotely sensed data. *Atmospheric Research* 144:4–20.
- REGAN, T. J., L. L. MASTER, AND G. A. HAMMERSON. 2004. Capturing expert knowledge for threatened species assessments: a case study using NatureServe conservation status ranks. *Acta Oecologica* 26:95–107.
- R CORE TEAM. 2021. R: a language and environment for statistical computing. Version 4.1.1. R Foundation for Statistical Computing, Vienna, Austria.
- RICHARDSON, C. J. 2010. The Everglades: North America’s subtropical wetland. *Wetlands Ecology and Management* 18:517–542.
- RICHMOND, O. M., J. TECKLIN, AND S. R. BEISSINGER. 2008. Distribution of California Black Rails in the Sierra Nevada foothills. *Journal of Field Ornithology* 79:381–390.
- RICHMOND, O. M., S. K. CHEN, B. B. RISK, J. TECKLIN, AND S. R. BEISSINGER. 2010. California Black Rails depend on irrigation-fed wetlands in the Sierra Nevada foothills. *California Agriculture* 64(2):85–93.
- ROACH, N. S., AND K. BARRETT. 2015. Managed habitats increase occupancy of Black Rails (*Laterallus jamaicensis*) and may buffer impacts from sea level rise. *Wetlands* 35:1065–1076.
- SAH, J. P., M. S. ROSS, S. SAHA, P. MINCHIN, AND J. SADLE. 2014. Trajectories of vegetation response to water management in Taylor Slough, Everglades National Park, Florida. *Wetlands* 34:65–79.
- SIVULA, T., M. MAGNUSSON, AND A. VEHTARI. 2022. Unbiased estimator for the variance of the leave-one-out cross-validation estimator for a Bayesian normal model with fixed variance. *Communications in Statistics-Theory and Methods* 51:in press. DOI: 10.1080/03610926.2021.2021240
- SHEPARD, M. K., B. A. CAMPBELL, M. H. BULMER, T. G. FARR, T.G. GADDIS, AND J. J. PLATT. 2001. The roughness of natural terrain: a planetary and remote sensing perspective. *Journal of Geophysical Research: Planets* 106:32777–32795.
- SLOCUM, M. G., W. J. PLATT, AND H. C. COOLEY. 2003. Effects of differences in prescribed fire regimes on patchiness and intensity of fires in subtropical savannas of Everglades National Park, Florida. *Restoration Ecology* 11:91–102.
- TSAO, D. C., J. Y. TAKEKAWA, I. WOO, J. L. YEE, AND J. G. EVENS. 2009. Home range, habitat selection, and movements of California Black Rails at tidal marshes at San Francisco Bay, California. *Condor* 111:599–610.

- U.S. FISH AND WILDLIFE SERVICE. 2020. Endangered and Threatened Wildlife and Plants; Threatened Species Status for Eastern Black Rail With a Section 4(d) Rule. Federal Register 85:63764–63803.
- VAN SCHMIDT, N. D., T. KOVACH, A. M. KILPATRICK, J. L. OVIEDO, L. HUNTSINGER, T. HRUSKA, N. L. MILLER, AND S. R. BEISSINGER. 2019. Integrating social and ecological data to model metapopulation dynamics in coupled human and natural systems. *Ecology* 100:e02711.
- VEHTARI, A., A. GELMAN, AND J. GABRY. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing* 27:1413–1432.
- VITOUSEK, S., P. L. BARNARD, C. H. FLETCHER, N. FRAZER, L. ERIKSON, AND C. D. STORLAZZI. 2017. Doubling of coastal flooding frequency within decades due to sea-level rise. *Scientific Reports* 7(1):1–9.
- WATTS, B. D. 2016. Status and distribution of the Eastern Black Rail along the Atlantic and Gulf Coasts of North America. The Center for Conservation Biology Technical Report Series, CCBTR-16-09. College of William and Mary/Virginia Commonwealth University, Williamsburg, Virginia.
- WATTS, B. D. 2021. Breeding phenology of the Eastern Black Rail (*Laterallus jamaicensis*). *Wilson Journal of Ornithology* 132:1043–1047.
- WATTS, B. D., D. F. BRINKER, M. D. WILSON, F. M. SMITH, AND C. H. HINES. 2021. Decline of Eastern Black Rails (*Laterallus jamaicensis jamaicensis*) within the Chesapeake Bay Region, USA. *Waterbirds* 44:257–267.
- WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. *Ornithological Monographs* 8:1–93.

Appendix A. Occupancy status during 2020 and 2021 and habitat characteristics at all survey plots measured in South Florida.							
Point	Status	Dominant species	Mean cover	Mean height of tallest vegeta- tion	Percentage satu- rated soil	Percent shallow water (1–3 cm)	Roughness
BC-16	unoccupied	sawgrass	91.1	63.0	0%	0%	0.10
BC-30	occupied	gulf hairawn muhly	87.9	47.0	52%	0%	0.10
BC-31	occupied	gulf hairawn muhly	84.0	45.5	68%	8%	0.22
BC-50	occupied	gulf hairawn muhly	68.0	42.2	44%	8%	0.38
BC-52	occupied	gulf hairawn muhly	87.1	43.3	36%	24%	0.16
BC-54	occupied	gulf hairawn muhly	96.0	49.0	80%	8%	0.10
BC-55	occupied	sawgrass	68.5	40.0	40%	16%	0.23
BC-56	occupied	sawgrass	89.5	52.7	28%	4%	0.18
BC-59	occupied	gulf hairawn muhly	82.5	59.0	28%	0%	0.19
BC-60	unoccupied	gulf hairawn muhly	80.5	46.0	36%	4%	0.24
BC-61	occupied	gulf hairawn muhly	81.5	54.0	20%	8%	0.34
BC-64	unoccupied	southern beaksedge	88.2	52.0	4%	0%	1.09
EV-01	unoccupied	southern beaksedge	70.4	32.0	12%	0%	0.13
EV-02	occupied	sawgrass	81.0	67.7	40%	4%	0.21
EV-03	occupied	Florida bluestem	92.5	43.0	12%	0%	0.10
EV-05	unoccupied	Florida bluestem	82.5	38.0	0%	0%	0.13
EV-07	unoccupied	bushy bluestem	76.5	33.0	40%	0%	0.30
EV-10	occupied	sawgrass	90.5	60.0	12%	4%	0.43
EV-23	unoccupied	black needlerush	26.0	20.0	0%	0%	0.10
EV-26	occupied	sawgrass	66.5	50.0	72%	24%	0.08
EV-26.7	occupied	sawgrass	76.0	46.0	80%	4%	0.08
EV-28.5	occupied	sawgrass	73.0	42.0	60%	16%	0.17
EV-29	occupied	sawgrass	62.0	51.1	80%	20%	0.09
EV-33	unoccupied	Florida bluestem	27.0	35.0	84%	0%	0.14
EV-35	unoccupied	sawgrass	56.5	38.7	0%	0%	0.08

Appendix A. (Continued) Occupancy status during 2020 and 2021 and habitat characteristics at all survey plots measured in South Florida.

Point	Status	Dominant species	Mean cover	Mean height of tallest vegeta- tion	Percentage satu- rated soil	Percent shallow water (1–3 cm)	Roughness
EV-36	unoccupied	sawgrass	61.0	58.8	0%	28%	0.12
EV-37	unoccupied	sawgrass	53.0	62.2	0%	0%	0.09
EV-41	unoccupied	sawgrass	82.5	42.0	0%	0%	0.07
EV-42	unoccupied	black needlerush	94.5	53.3	0%	0%	0.07
EV-44	unoccupied	sawgrass	68.0	57.0	0%	4%	0.09
EV-54	unoccupied	sawgrass	55.5	58.5	0%	0%	0.19
SG-21	occupied	sawgrass	76.5	44.0	24%	0%	0.08
SG-29	unoccupied	sawgrass	78.6	67.0	64%	36%	0.14
SG-31	unoccupied	sawgrass	70.0	62.5	0%	44%	0.11
SG-32	occupied	sawgrass	58.0	53.7	0%	0%	0.65
SG-75	unoccupied	sawgrass	48.5	34.4	56%	0%	0.18
SG-77	occupied	sawgrass	83.0	56.6	80%	0%	0.13
SG-78	unoccupied	sawgrass	87.5	80.0	64%	0%	0.18
SG-79	occupied	sawgrass	89.5	89.0	72%	0%	0.19
SG-80	unoccupied	sawgrass	59.0	32.0	45%	0%	0.12

**COMPARING THE FREQUENCY OF INCEST
BETWEEN SIBLINGS IN TWO POPULATIONS OF
FLORIDA SCRUB-JAYS (*Aphelocoma coerulescens*)**

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Extensive inbreeding can lead to inbreeding depression with deleterious effects on fitness and long-term population survival (Keller and Waller 2002). However, some level of inbreeding may be neutral or beneficial (Shields 1982, Kokko and Ots 2006, Szulkin et al. 2013). Nonetheless, avoiding incest is important for many species, particularly where populations are small or fragmented and the effects of inbreeding may be exacerbated (Lacy 1993).

Incest avoidance is often studied in the context of sociable species with high philopatry, such as cooperative breeders, where the potential for incest is high (Brown 1978). Many avian species appear to have mechanisms to avoid incest. For example, in cooperatively breeding Red-Cockaded Woodpeckers (*Dryobates borealis*), breeding females often disperse from their breeding territory after the death of their mates, thus avoiding pairing incestuously with their sons who may inherit the territory (Walters et al. 1988). Similarly, the cooperative and sometimes communally nesting Acorn Woodpecker (*Melanerpes formicivorus*) effectively avoids incest in several ways: females refrain from breeding in their natal family groups if their fathers are still present, and young birds disperse alone or in unisexual units, reducing the risk of siblings breeding together after dispersal (Koenig and Pitelka 1979). Kin recognition may also be an important factor in incest avoidance for cooperatively breeding species (Riehl and Stern 2015).

It is unclear if these apparent incest avoidance mechanisms are traits evolved through natural selection to reduce the risk of inbreeding or merely a benefit of behaviors selected to serve another function (Koenig and Haydock 2004). In this note, we compare rates of incest between siblings from two populations of Florida Scrub-Jays (*Aphelocoma coerulescens*) and suggest that habitat fragmentation may explain the differences.

Florida Scrub-Jays are a cooperatively breeding species endemic to the oak scrub of Florida. Breeding pairs defend territories year-round.

These territories are generally contiguous, with distinct, aggressively defended boundaries (Woolfenden and Fitzpatrick 1996). Territories are composed of a breeding pair and up to six non-breeding helpers, which are usually their offspring from previous years (Woolfenden and Fitzpatrick 1984). These helpers may remain at their natal territory for several years and overlap inhabiting the territory with their older and younger siblings.

Adult Florida Scrub-Jays are relatively long-lived and disperse short distances. Breeder survival is high (78%), as is survival of male non-breeders (81%; Woolfenden and Fitzpatrick 1984, 2014). Female non-breeders have lower survival (65%), likely owing to female-biased dispersal (Woolfenden and Fitzpatrick 1984, 2014). Florida Scrub-Jay females disperse farther and earlier than males (Woolfenden and Fitzpatrick 1984, Coulon et al. 2010, Aguillon et al. 2017, Suh et al. 2020). Females primarily gain a breeding position by replacing a female breeder at another territory, whereas males may inherit all or part of their natal territory (Woolfenden and Fitzpatrick 1996). The longest recorded Florida Scrub-Jay dispersal was 35 km, but 80% of dispersals are within 0.4 km of the natal territory (Woolfenden and Fitzpatrick 1984, 1996; Stith et al. 1996; Miller et al. 2021). Both male and female Florida Scrub-Jays that disperse more than two territories (0.8 km) from their natal site have significantly decreased survival and produce fewer offspring than those that become breeders near their natal territory (Fitzpatrick and Bowman 2016).

Florida Scrub-Jays are behaviorally and genetically monogamous (Quinn et al. 1999, Townsend et al. 2011) and appear to avoid pairing with close relatives. Incest is costly in this species; breeding pairs with larger proportions of their genome identical by descent suffer increased hatch failure (Chen et al. 2016). In nearly all cases, opposite-sex siblings in the same territory avoid pairing with each other, and breeders refrain from pairing with their offspring after the loss of a mate (Woolfenden and Fitzpatrick 2014). Woolfenden and Fitzpatrick (1984) report only five cases of incest in Florida Scrub-Jays. Four of those cases (80%) involved related individuals that never overlapped temporally in their natal territory; thus, they were presumably unaware of their genetic relationship. The fifth case of incest involved a short-lived mother-son pairing that produced fertile eggs before the female died during incubation. No cases of sibling-sibling pairings have been documented in the literature previously (Woolfenden and Fitzpatrick 1996). Woolfenden and Fitzpatrick (1984) believe that Florida Scrub-Jays most likely avoid incest by refusing to pair with members of their natal territory (an incest taboo), rather than actively recognizing and avoiding close genetic relatives. There is no evidence

that Florida Scrub-Jays have an alternative way of identifying genetic relatives.

The Florida Scrub-Jay populations at Avon Park Air Force Range (APAFR) and Archbold Biological Station (ABS) are closely studied. Virtually all Florida Scrub-Jays at APAFR and ABS are banded with a unique combination of colored bands, nests are found, nestlings banded, and individual relationships and movements are well-documented (Woolfenden and Fitzpatrick 1984, Chen et al. 2016, Fitzpatrick and Bowman 2016).

The APAFR is a roughly 43,000-ha military training facility located in Highlands and Polk counties, Florida. The scrub on APAFR occurs on multiple, discontinuous ridges embedded in a matrix of forests, which pose a significant dispersal barrier to Florida Scrub-Jays (Stith et al. 1996), resulting in areas of scrub that are isolated from the others. Florida Scrub-Jays at APAFR disperse greater distances than those at ABS because they must cross non-scrub gaps (Coulon et al. 2010). Archbold Biological Station is a roughly 2,000-ha research facility located in Highlands County, Florida composed of approximately 1,700 ha of contiguous scrub (Fig. 1). Although the area monitored at ABS is 40% of the size of Florida Scrub-Jay habitat at APAFR, nearly all of it is occupied by jays (60–80 territories), whereas much of the scrub at APAFR is not (40–50 territories; Fig. 1).

During the 2021 breeding season at APAFR, we observed a sibling-sibling pair that successfully fledged a full clutch of three young, all of which survived beyond nutritional independence. After observing this surprising case of full sibling incest, we searched the historical nest records at APAFR (1994–2021) and ABS (1971–2021) for other examples of jays that share at least one parent mating. We identified unique breeding pairs for which the natal nest, and thus parentage, of both members of the breeding pair was known to identify pairings between siblings (Table 1). For each occurrence of sibling incest, we counted the number of unpaired males and females on neighboring territories, noted if the siblings overlapped on the natal territory, and described any previous dispersal attempts or movements. Then we compared the incidence rate of sibling incest (all observations and taboo-violating only [overlapped on natal territory]) at APAFR and ABS using a two-sample, one-tailed test for equality of proportions. Some authors recommend a continuity correction when fewer than 5 instances of an observation exist (Newcombe 1998); however, others consider this too conservative (Larntz 1978), thus we present results both ways.

Incest between siblings is rare in both Florida Scrub-Jay populations studied (Table 1), but it is more frequent at APAFR than ABS (uncorrected: $\chi^2 = 3.5$, $df = 1$, $P = 0.03$; continuity corrected: $\chi^2 = 2.5$,

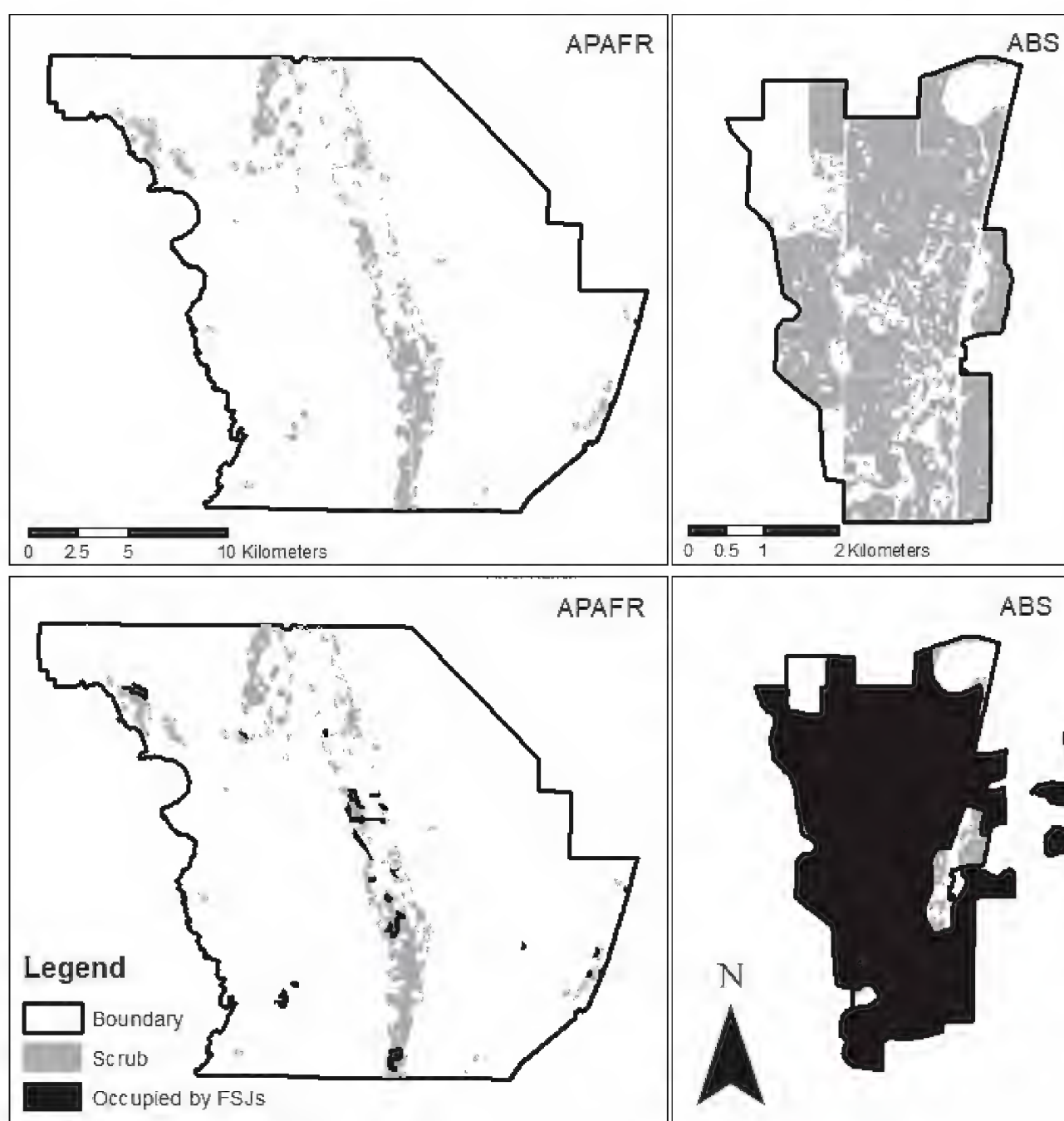


Figure 1. Avon Park Air Force Range (APAFR; left) and Archbold Biological Station (ABS; right) in central Florida where we studied incest in Florida Scrub-Jays using historical data from 1971–2021. Land cover types differed between study areas (top). Because much of the scrub at APAFR is not occupied by Florida Scrub-Jays (FSJs) and the ridges of scrub are isolated, jays exist in small, fragmented subpopulations there (bottom left), whereas at ABS, their territories are contiguous (bottom right).

$df = 1, P = 0.06$). At ABS only one of the four observations would violate an incest taboo (Table 1). In this instance one sibling was observed helping at the natal nest of the other. At APAFR 40% of the observations of sibling incest occurred between siblings who overlapped on their natal territories, thus violating an incest taboo (Table 1). However, the observed differences between sites in the frequency of taboo-violating occurrences of incest were not statistically significant (uncorrected: $\chi^2 = 2.2, df = 1, P = 0.07$; continuity corrected: $\chi^2 = 1.1, df = 1, P = 0.15$).

Table 1. Observations of sibling incest in Florida Scrub-Jays in central Florida at Avon Park Air Force Range (APAFR) during 1994–2021 and at Archbold Biological Station (ABS) during 1971–2021. We defined incest as violating taboo if the siblings had been on their natal territory at the same time.

	APAFR		ABS	
	Count	Percent	Count	Percent
Unique pairs with known parentage	381		434	
Unique sibling pairs	10	2.62%	4	0.92%
No taboo	6	60.00%	3	75.00%
Violate taboo	4	40.00%	1	25.00%

Mate availability is not the limiting factor resulting in violations of the incest taboo. While incest may arise when few unrelated and unpaired birds are available, in all instances we observed (at both APAFR and ABS), unrelated helpers of both sexes resided at neighboring or nearby territories.

We suggest that habitat fragmentation may explain the observed difference in rates of sibling incest between APAFR and ABS. In systems where incest avoidance is primarily achieved through dispersal away from the natal patch, fragmentation may increase the frequency of incest by increasing dispersal costs such that individuals do not disperse away from their natal patch or by reducing the number of patches to disperse to, thereby increasing the probability that individuals from the same natal patch disperse to the same patch. Seventy percent (7/10) of cases of sibling incest at APAFR involved females from a geographically isolated natal patch of scrub remaining there to breed rather than dispersing. Two additional cases at APAFR and one at ABS involved females who moved territories multiple times attempting to secure a breeding position prior to mating with a sibling. Thus 90% of the observed instances of incest between siblings at APAFR were associated with avoiding long-distance dispersals or additional multiple-step dispersals.

We expected that female Florida Scrub-Jays in fragmented landscapes might be willing to break the incest taboo in the face of high dispersal costs. However, the frequency of taboo-violating instances of incest did not differ statistically between APAFR and ABS. This suggests that the observed differences in the rates of incest are not due to behavioral differences in adhering to an incest taboo but rather consequences of differences in dispersal patterns between fragmented and contiguous landscapes.

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LITERATURE CITED

- AGUILLON, S. M., J. W. FITZPATRICK, R. BOWMAN, S. J. SCHOECH, A. G. CLARK, AND N. CHEN. 2017. Deconstructing isolation-by-distance: the genomic consequences of limited dispersal. *PLoS Genetics* 13:1–27.
- BROWN, J. L. 1978. Avian communal breeding systems. *Annual Review of Ecology and Systematics* 9:123–155.
- CHEN, N., E. J. COSGROVE, R. BOWMAN, J. W. FITZPATRICK, AND A. G. CLARK. 2016. Genomic consequences of population decline in the endangered Florida Scrub-Jay. *Current Biology* 26:2974–2979.
- COULON, A., J. W. FITZPATRICK, R. BOWMAN, AND I. J. LOVETTE. 2010. Effects of habitat fragmentation on effective dispersal of Florida Scrub-Jays. *Conservation Biology* 24:1080–1088.
- FITZPATRICK, J. W., AND R. BOWMAN. 2016. Florida Scrub-Jay: oversized territories and group defense in a fire-maintained habitat. Pages 77–96 *in* Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior (W. D. Koenig, and J. L. Dickinson, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- KELLER, L. F., AND D. M. WALLER. 2002. Inbreeding effects in wild populations. *Trends in Ecology & Evolution* 17:230–241.
- KOENIG, W. D., AND J. HAYDOCK. 2004. Incest and incest avoidance. Pages 142–156 *in* Ecology and Evolution of Cooperative Breeding in Birds (W. D. Koenig and J. L. Dickinson, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- KOENIG, W. D., AND F. A. PITELKA. 1979. Relatedness and inbreeding avoidance: counterplays in the communally nesting Acorn Woodpecker. *New Series* 206:1103–1105.
- KOKKO, H., AND I. OTS. 2006. When not to avoid inbreeding. *Evolution* 60:467–475.
- LACY, R. C. 1993. Impacts of inbreeding in natural and captive populations of vertebrates: implications for conservation. *Perspectives in Biology and Medicine* 36:480–496.
- LARNTZ, K. 1978. Small-sample comparisons of exact levels for chi-squared goodness-of-fit statistics. *Journal of the American Statistical Association* 73:253–263.
- MILLER, K. E., R. RISCH, AND J. GARCIA. 2021. Long-distance dispersal in a sedentary species, *Aphelocoma coerulescens* (Florida Scrub-Jay), in Northern Florida. *Southeastern Naturalist* 20:N37.
- NEWCOMBE, R. G. 1998. Interval estimation for the difference between independent proportions: comparison of eleven methods. *Statistics in Medicine* 17:873–890.
- QUINN, J. S., G. E. WOOLFENDEN, J. W. FITZPATRICK, AND B. N. WHITE. 1999. Multi-locus DNA fingerprinting supports genetic monogamy in Florida Scrub-Jays. *Behavioral Ecology and Sociobiology* 45:1–10.
- RIEHL, C., AND C. A. STERN. 2015. How cooperatively breeding birds identify relatives and avoid incest: new insights into dispersal and kin recognition. *BioEssays* 37:1303–1308.
- SHIELDS, W. M. 1982. Philopatry, inbreeding, and the evolution of sex. State University of New York Press, Albany.
- STITH, B. M., J. W. FITZPATRICK, G. E. WOOLFENDEN, AND B. PRANTY. 1996. Classification and conservation of metapopulations: a case study of the Florida scrub-jay. Pages 187–215 *in* Metapopulations and Wildlife Conservation (D. R. McCullough, Ed.). Island Press, Washington, D.C.

- SUH, Y. H., M. B. PESENDORFER, A. TRINGALI, R. BOWMAN, AND J. W. FITZPATRICK. 2020. Investigating social and environmental predictors of natal dispersal in a cooperative breeding bird. *Behavioral Ecology* 31:692–701.
- SZULKIN, M., K. V. STOPHER, J. M. PEMBERTON, AND J. M. REID. 2013. Inbreeding avoidance, tolerance, or preference in animals? *Trends in Ecology and Evolution* 28:205–211.
- TOWNSEND, A. K., R. BOWMAN, J. W. FITZPATRICK, M. DENT, AND I. J. LOVETTE. 2011. Genetic monogamy across variable demographic landscapes in cooperatively breeding Florida Scrub-Jays. *Behavioral Ecology* 22:464–470.
- WALTERS, J. R., P. D. DOERR, AND J. H. CARTER. 1988. The cooperative breeding system of the Red-Cockaded Woodpecker. *Ethology* 78:275–305.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1984. *The Florida Scrub Jay: Demography of a Cooperative-Breeding Bird*. Princeton University Press, Princeton, New Jersey.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1996. Florida Scrub-Jay (*Aphelocoma coerulescens*). Account in *The Birds of North America* (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania and The American Ornithologists' Union, Washington, D.C.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 2014. Sexual asymmetries in the life history of the Florida Scrub Jay. Pages 87–107 in *Ecological aspects of social evolution* (D. I. Rubenstein and R. W. Wrangham, Eds.). Princeton University Press, Princeton, New Jersey.

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CURRENT DISTRIBUTION OF BLACK RAILS IN FLORIDA

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Abstract.—The Eastern Black Rail (*Laterallus jamaicensis jamaicensis*) subspecies has experienced drastic contemporary regional population declines and in 2020 was federally listed as Threatened under the Endangered Species Act. Population trends in much of its range remain unknown, however, because it is understudied and notoriously difficult to detect. Florida is presumed to be one of the remaining strongholds for the Eastern Black Rail, but a population survey has not been conducted in more than two decades. We conducted 1,314 Black Rail surveys at 438 points in 2016 and 2017 throughout Florida, and an additional 731 surveys at 287 points in 2020 in South Florida. We detected Black Rails at just 39 points on 15 of the 28 (54%) surveyed public properties during all three survey years. Six additional properties are currently occupied by Black Rails, as indicated by opportunistic sighting records from other trained biologists during the past ten years, resulting in 21 total occupied properties in 19 Florida counties. Occupancy and detection rates were too low to allow for any formal statistical analysis of the survey data. The timing, location, and frequency of our surveys may have contributed to the lack of detections during our surveys, and more work is needed to understand how best to survey this elusive species. Nevertheless, it seems likely that the paucity of detections is at least in part due to the rarity of the species, and intensive monitoring, research, and management will likely be needed to recover the species.

Key words: Black Rail, Florida, survey

The Eastern Black Rail (*Laterallus jamaicensis jamaicensis*) is one of two subspecies in North America (Eddleman et al. 2020). Its current range extends south along the Atlantic Coast states from New Jersey and across the Gulf coast from Florida to Texas. There are also populations in interior states in Kansas, Oklahoma, and Colorado. Eastern Black Rail populations have declined over the past several decades, some at a rapid rate (Watts 2016). Although detailed historical range-wide data are sparse for this highly secretive marshbird, systematic surveys conducted in the Chesapeake Bay region show an annualized rate of decline in occupancy of 6.5% from 1990 to 2014 (Watts et al. 2021). This pattern may be repeating itself throughout the Atlantic states (Watts 2016). The trend is largely unknown in Gulf and interior states, although it does appear there have been extirpations from some of the northernmost states in which the species used to occur (Watts 2016). In 1990, the Eastern Black Rail was considered a species of highest concern by Florida state biologists (Millsap et al. 1990), and in 2020 the United States Fish and Wildlife Service listed the subspecies as threatened under the Endangered Species Act (USFWS 2020). Understanding the current distribution of Black Rails in Florida provides baseline information that allows researchers and conservationists to compare to historical records and track future trends.

Black Rails are North America's smallest and ostensibly most secretive rails. They are cryptically colored and prefer to move through marsh vegetation on the ground as opposed to flying. Although they occur in fresh, brackish, and salt marshes, they are restricted to shallow water (<6 cm) for breeding and foraging (Eddleman et al. 2020). Breeding habitats typically are a matrix of vegetation that provides dense cover with an open understory near or over open water (Eddleman et al. 2020, Flores and Eddleman 1995, Legare and Eddleman 2001), with vegetation structure being more predictive of bird presence than species composition (Flores and Eddleman 1995). While Black Rails are mostly associated with grassy species, such as *Spartina bakeri*, *Cladium jamaicense*, rushes (*Scirpus* spp.), sedges (*Schoenoplectus pungens*, *Carex* spp.), and cattails (*Typha* spp.) in freshwater marshes and *Spartina* species in salt marshes (ACJV 2020), they have also been associated with rushes such as black needlerush (*Juncus roemerianus*) in salt marshes and mixed-herbaceous species in wet prairies (A. C. Schwarzer, Florida Fish and Wildlife Conservation Commission [FWC], unpublished data). Like most rail species, they lay large clutches (7.6 ± 1.3 SD, range = 4–13 [Eddleman et al. 2020]). Independent young often disperse <10 km; although, they are capable of dispersing longer distances (Hall et al. 2018).

Black Rail distributions within Florida are not well understood. Historically, Black Rails have been detected during the breeding season at multiple salt and freshwater marsh locations in Florida (Runde et al. 1990, Watts 2016). However, the only systematic survey data available was more than two decades old and survey coverage was limited, in particular for interior freshwater marshes, compared to the amount of possible habitat (Runde et al. 1990). The objectives of this study were to 1) conduct a large-scale survey on historically occupied and previously unsurveyed areas to estimate occupancy rates, and 2) aggregate data from other sources to describe the overall distribution of Black Rails in Florida.

METHODS

To establish the distribution of Eastern Black Rails in Florida, we conducted standardized call playback surveys in 2016, 2017, and 2020. We conducted the first set of surveys across the state during the core of the breeding season, April to July (Legare and Eddleman 2001) excluding the period when chicks and juveniles are often heard in August, in 2016 and 2017. We then conducted additional surveys in south Florida in 2020 that expanded coverage on already-surveyed areas and explored new areas that were not covered in 2016 and 2017. We conducted the 2020 surveys in February because the breeding season in South Florida likely begins earlier than in other areas of the state, given the hydrological cycle in that region. The Everglades typically enter a dry period from November–May (Abiy et al. 2019), which by late January provides ample shallow water areas favored by rails for breeding. The dry period is followed by a wet season (Abiy et al. 2019) that likely precludes breeding during the time of year when breeding is typically observed in other parts of Florida because of deep water conditions. We also compiled and report records of standardized multi-species marshbird surveys and opportunistic detections from state wildlife biologists for the past decade (2011–2020), including those applicable records already reported in Ward et al. (2016).

Site selection.—For the 2016 and 2017 surveys, we used two approaches to select potential areas and survey sites within those areas. Initially, we tried to predict Black Rail habitat with a spatial model using publicly available data; however, the model had poor success in identifying appropriate Black Rail habitat (i.e., it failed to identify habitat in areas with known Black Rail occupancy). Therefore, we visually inspected aerial and satellite imagery and identified sites on areas that were similar to known occupied sites. For saltwater and brackish sites, this included areas of high marsh that were composed of a matrix of several types and heights of vegetation, small areas of open water, and salt or sand flats. In freshwater, this included 1) small discrete wetlands with largely non-woody vegetative cover along the wetland edges embedded in generally open landscapes (e.g., wet prairie) or 2) higher elevation, mixed non-woody vegetation patches within larger wetland complexes. Within chosen survey areas, we randomly generated >2,500 survey points that were ≥ 400 m apart to maximize the overall spatial coverage of the survey. We used a second visual inspection to confirm the presence of potentially suitable habitat to reduce the number of potential points to $\sim 1,000$. We then ground-truthed points prior to conducting surveys to verify that the points were accessible and within potential Black Rail habitat. The number of survey points per survey area varied based on the amount of accessible potential habitat.

For the 2020 surveys, we systematically placed points along accessible roads to minimize travel time between points and maximize number of points surveyed in a day. We

did not randomize point locations as we did in 2016 and 2017 surveys because the intent of the surveys was to rapidly assess south Florida sites that were not adequately covered in the prior survey timeframe.

Field methods.—Avian Research and Conservation Institute (ARCI), FWC, National Wildlife Refuge (NWR), and Center for Conservation Biology (CCB) staff conducted all standardized surveys. We surveyed points one to three times per breeding season, which is substantially less than what is recommended to establish the presence of Black Rails at a given point because of low detection rates (Tolliver et al. 2019), but this number of visits allowed us to maximize the spatial extent of the survey. We arranged points in routes, with each route consisting of 5–16 points each, representing the number that could be surveyed in a single morning or evening within the appropriate timeframe (see below). We did not sample points across years because surveys were intended to maximize geographic coverage. We conducted Black Rail surveys using a standardized call playback technique (Conway 2011) modified specifically for Black Rails (Wilson et al. 2009). The call playback survey was a 10-min sequence of alternating silent listening periods and species playback in the following order: 1) 2-min silence, 2) 4-min Black Rail calls, 3) 1-min silence, 3) 2-min Clapper Rail (*Rallus crepitans*) calls, and 4) 1-min silence. This standardized protocol was also used for surveys conducted in New Jersey, Maryland, Virginia, North Carolina, South Carolina, and Georgia. We conducted counts in weather conducive to detecting birds, which excluded periods of rain, wind velocities >20 km/hr, or high ambient noise. All fieldwork was conducted in accordance with the ethical considerations outlined in Fair et al. (2010).

We initially located each point with a global positioning system unit and marked it with flagging for the subsequent surveys. A single trained observer conducted all surveys between 0.5–1 hour before sunrise and 3 hours after sunrise or in the evening starting 3 hours before sunset to 0.5–1 hour after sunset. We recorded temperature, weather, noise level, and wind speed at each point. Once the playback began, we recorded all detections within 1-min intervals until the end of the survey. We recorded all Black Rails heard or seen from the point and noted the type of call. We measured distance to each bird's estimated position with a laser rangefinder or estimated distance visually if rangefinders were not available. We also recorded the presence and number of certain incidental species (Virginia Rail [*Rallus limicola*], Yellow Rail [*Coturnicops noveboracensis*], Clapper Rail, King Rail [*R. elegans*], Least Bittern [*Ixobrychus exilis*], Seaside Sparrow [*Ammodramus maritima*], and Marsh Wren [*Cistothorus palustris*]) during the survey.

RESULTS

We conducted 1,314 surveys at 438 points (i.e., all points received three surveys) in 2016 and 2017. Survey data from 11 points at St. Johns NWR were misplaced, resulting in data from 1,287 surveys at 429 points. However, we were able to confirm that St. Johns NWR was occupied during the survey period. We detected rails at 21 of 429 points. Twelve detections occurred in April, 7 in May, and 13 in June. The number of survey points per area ranged from 5–51. We conducted 731 surveys at 287 points ($\bar{x} = 2.55$ surveys/point) across four areas in 2020. We found birds at 18 of 287 points. We were unable to estimate occupancy because of the very small number of detections. Thus, we report Black Rail presence by property because habitat management priorities are often developed at the property scale, i.e., the presence of an imperiled species on a property can influence decisions by property owners and managers.

We found Black Rails on 15 of 28 properties surveyed specifically for Black Rails (Table 1; Fig. 1). Data from standardized multispecies surveys indicated that an additional two properties were also occupied, bringing the total to 17 occupied properties according to standardized surveys. We found that four of the five properties reported by Runde et al. (1990) as being occupied were still currently occupied (Table 1). Lake Woodruff NWR was the only historically occupied property where we did not detect any birds. In addition, we did not always observe Black Rails at the same location or units within those properties as Runde et al. (1990). For instance, Runde et al. (1990) reported detections at two of four general locations within St. Marks NWR, whereas we found rails at only one of these. In Big Bend Wildlife Management Area (WMA), Runde et al. (1990) reported detections at the Jena and Tide Swamp Units, whereas we only detected Black Rails at the Hickory Mound Unit. Incidental observations during the breeding season in 2015 confirmed that Black Rails still occupy the Jena Unit, but we did not detect them during standardized surveys.

In addition to standardized Black Rail surveys, we compiled opportunistic observations by trained biologists throughout the state within the past 10 years, which brought the number of occupied properties to 21 (Table 2). With standardized and nonstandardized data combined, Black Rails were detected in 19 counties out of 25 counties surveyed.

Everglades National Park, Francis Taylor and Everglades WMAs, Big Cypress National Preserve, and St. Vincent NWR had the highest number of total individual detections. However, we do not report numbers of birds because the individuals may be detected at the same point on different days. In addition, data for St. Johns NWR, a known Black Rail hotspot, were lost and the exact number of birds detected and points occupied is unknown for this property.

DISCUSSION

The precipitous decline of the Eastern Black Rail combined with the lack of contemporary data in Florida created an urgent need for a statewide survey that has filled important data gaps related to the distribution of Black Rail in Florida. Watts (2016) reported 13 counties with possible or probable breeding records since 2010, whereas we found rails in 19 counties. Our count remains lower than the 32 counties reported historically (Watts 2016), but the historical data range from the late 1800s to 2010, which is a much longer temporal period than our study, and not all counties were covered during our surveys, particularly in the southwest part of the state. Twenty-four of the 25 counties we surveyed were among those 32 reported historically,

Table 1. Sites or properties surveyed for Black Rails (BLRA) during 2013–2020 breeding seasons in Florida. Type of survey: B = Black Rail-specific protocol, M = multi-species secretive marshbird surveys. Type of wetland: F = freshwater, S = saltwater, B = brackish.

Property or site - standardized surveys	Year(s) surveyed	Type of survey	Number of points with BLRA detected	Number of total survey points	Type of wetland
Avon Park Air Force Range	2017	B	1	11	F
Big Bend Wildlife Management Area ^a	2016	B	1	46	S
Big Cypress National Preserve	2020	B	7	143	F
Buck Lake Conservation Area	2017	B	1	9	B
Canaveral Marshes Conservation Area	2017	B	2	10	B
Crystal River Preserve State Park	2016	B	0	7	S
Disney Wilderness Preserve	2016	B	0	9	F
Escape Ranch Conservation Easement	2017	B	0	10	F
Everglades National Park	2017, 2020	B	7	102 (94F/8S)	F/S
Fakahatchee Strand Preserve State Park	2020	B	0	16	F
Herky Huffman/Bull Creek Wildlife Management Area	2016	B	0	14	F
J. W. Corbett Wildlife Management Area	2013–2019	M	6	36	F
Jones/Hungryland Wildlife and Environmental Area	2014–2017, 2019	B, M	1	49	F
Kissimmee Prairie Preserve State Park	2016	B	0	29	F
Lake Woodruff National Wildlife Refuge ^a	2016	B	0	5	F
Myakka River State Park	2017	B	0	18	F
Salt Lake Wildlife Management Area	2017, 2019, 2020	B	3	9	B
South Dade Wetlands (includes the Everglades Mitigation Bank, Southern Glades and Model Lands Basin Conservation Areas)	2017, 2020	B	7	99	F
St. John National Wildlife Refuge ^a	2016	B	Unk ^b	9	B

^aHistorically occupied as reported in Runde et al. (1990).
^bBlack Rails were present but the datasheets were lost so the total number of detections is unknown.

Table 1. (Continued) Sites or properties surveyed for Black Rails (BLRA) during 2013–2020 breeding seasons in Florida. Type of survey: B = Black Rail-specific protocol, M = multi-species secretive marshbird surveys. Type of wetland: F = freshwater, S = saltwater, B = brackish.

Property or site - standardized surveys	Year(s) surveyed	Type of survey	Number of points with BLRA detected	Number of total survey points	Type of wetland
St. Marks National Wildlife Refuge ^a	2016	B	1	41	S
St. Vincent National Wildlife Refuge ^a	2016	B	7	25	S
T. Mabry Carlton, Jr. Memorial Reserve	2017	B	0	11	F
Tampa Bay Estuarine Ecosystem	2017	B	0	9	S
Terra Ceia Preserve State Park	2017	B	0	9	S
Three Lakes Wildlife Management Area	2016	B	1	28	F
Triple N Ranch Wildlife Management Area	2016	B	0	8	F
Weekiwachee Preserve (includes Linda Pederson/Jenkins Creek Park)	2017	B	1	31	S
Werner-Boyce Salt Springs State Park	2016	B	1	7	S

^aHistorically occupied as reported in Runde et al. (1990).
^bBlack Rails were present but the datasheets were lost so the total number of detections is unknown.

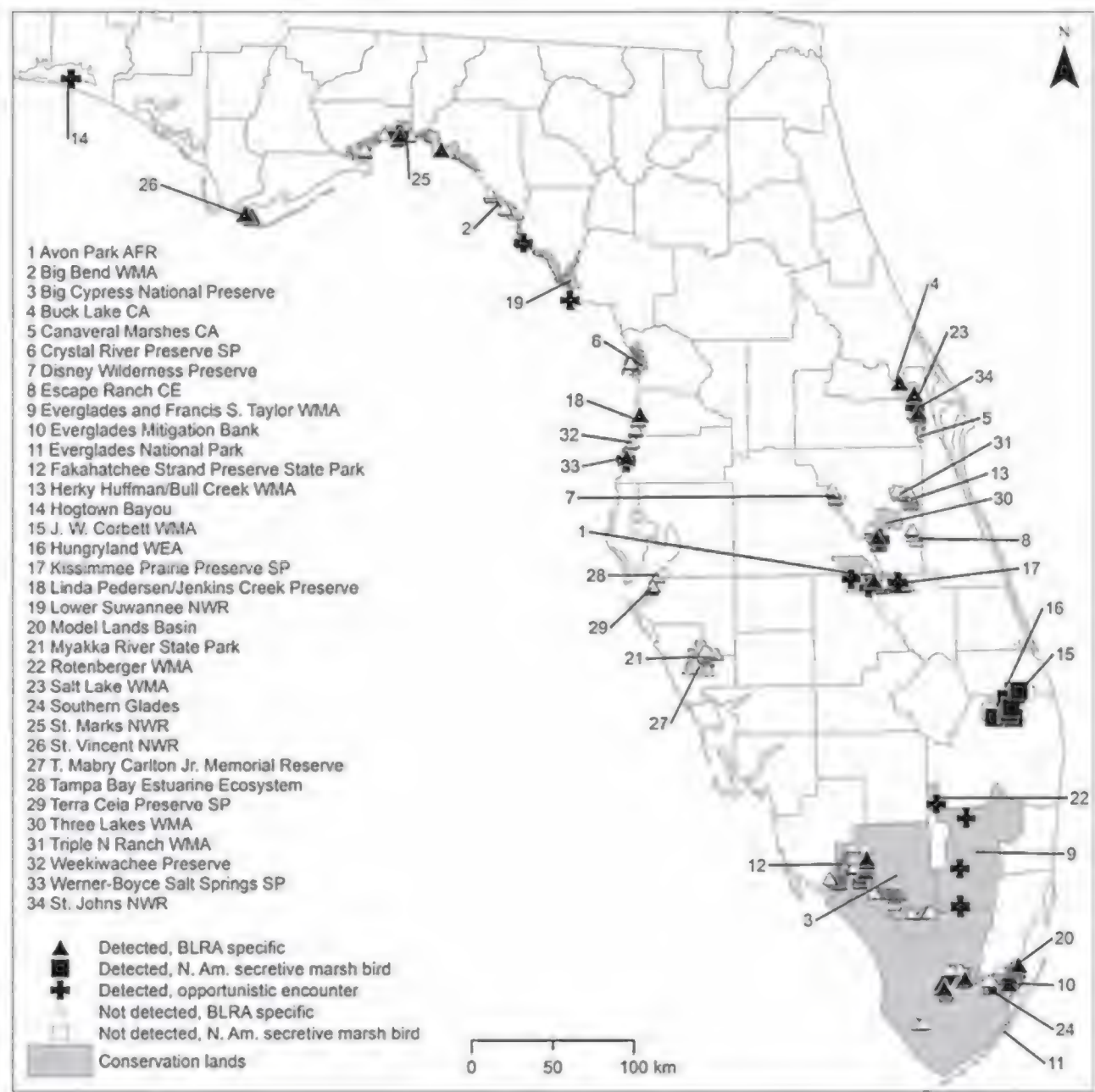


Figure 1. Sites surveyed for Black Rails (BLRA) in Florida during 2013–2020 using a Black Rail-specific survey protocol and multi-species North American (N. Am.) secretive marshbird surveys. Map also includes opportunistic detections of Black Rails from 2011–2020.

including 18 of the counties with Black Rail observations, while 1 (Martin County) was an entirely new record. Although we wished to have as broad a survey as possible, we did not survey any properties in 7 of 32 counties reported historically (Watts 2016) because the habitat was temporarily unsuitable (e.g., drought conditions) at the designated survey time or because of resource and time constraints.

Black Rails occurred across the state, from the Panhandle to the Everglades, yet densities appeared low at most sites. It was not possible to estimate the relative abundance of rails across properties or regions of the state because of differences in survey efforts and because the extremely low detection rates and variable data types precluded a

Table 2. Sites or properties with opportunistic detections of Black Rails by professional wildlife personnel during 2011–2020 breeding seasons in Florida, including the total number of unique points with detections. Type of wetland: F = freshwater, S = saltwater, B = brackish.

Property or site - non-standardized observations	Year(s) detected	Number of points with detections	Type of wetland
Avon Park Air Force Range	2017	2	F
Big Bend Wildlife Management Area	2015	1	S
Everglades and Francis S. Taylor Wildlife Management Area	2011, 2015, 2019	5	F
Hogtown Bayou	2011, 2015	2	S
Kissimmee Prairie Preserve State Park	2016	3	F
Lower Suwannee National Wildlife Refuge	2018	1	S
Rotenberger Wildlife Management Area	2012	1	F
St. Marks National Wildlife Refuge	2016	1	S
Three Lakes Wildlife Management Area	2015, 2018	8	F
Werner-Boyce Salt Springs State Park	2016	2	S

more rigorous analysis. We therefore suggest a cautious interpretation of our results in this respect. Overall, freshwater marshes, which had been largely overlooked in previous surveys, yielded a number of detections. It is our sense that there are both more birds and more high-quality rail habitat south of Okeechobee, but more research is needed to confirm this. The Upper St. Johns River basin, composed of St. Johns NWR, Canaveral Marshes and Buck Lake Conservation Areas, and Salt Lake Wildlife WMA, also had a number of points with rail detections, as did the central prairie region consisting of Three Lakes WMA, Kissimmee Prairie Preserve State Park, and Avon Park Air Force Range. Both regions have a number of surrounding properties, both public and private, that may yield additional detections. The Gulf Coast region, which had been considered one of the strongholds of the species in the state, had a broad distribution of points with Black Rail detections, but the numbers of points with detections appeared to be lower than in prior surveys (Runde et al. 1990).

Black Rail surveys in Texas indicated that 8 surveys are required to ensure a 95% probability of detection at a given point (Tolliver et al. 2019). Given the low detectability of Black Rails and comparatively low survey effort of 3 surveys per point, it is almost certain that rails occurred at points and properties where we did not encounter them. Thus, our results should be considered a conservative depiction of the distribution and occurrence of Black Rails in Florida. One possible explanation for this low encounter rate is that call playback for Black Rails is less effective than for other secretive marshbirds. One study of a different subspecies, the California Black Rail (*L. j. coturniculus*), indicated that

call playback increased the number of birds detected by only 13% over passive listening and that a minimum of five surveys per point and up to 15 surveys per point may be needed to attain >90% detection probability (Conway et al. 2004). This study suggests that Black Rails may not be as sensitive to playback as older studies have suggested (Legare et al. 1999), though even these older studies acknowledge that detection of an individual varies greatly by time of day, season, sex, and stage of nesting. These results imply that an observer may not detect birds if they were not already naturally vocalizing.

A second possibility is that the habitat selection by Black Rails limits their numbers. Black Rails build their nests within 0–6 cm of the ground and require shallow water to prevent flooding during nesting and to provide foraging habitat for chicks (Eddleman et al. 2020). In addition, Black Rails generally prefer a matrix of vegetation dominated by clumping plants that provide cover with an open understory (Legare and Eddleman 2001). The sites we surveyed had extensive marshes, but the particular hydrologic and structural conditions needed to support Black Rails likely exist in only a small portion of each of these marshes. Freshwater marshes in particular are subject to unpredictable temporal variation in water levels as a function of rainfall and temperature each breeding season. Individual sites may experience extirpation and recolonization on a regular basis, particularly if isolated, as has been observed in the Sierra Nevada foothills population of the California Black Rail (Hall et al. 2018).

Another possible reason for the low encounter rate is that our assumptions about Black Rail habitat could be improved. As discussed in the methods, spatial modeling approaches are currently limited by the data sets available, and we had to rely on expert opinion to identify potential habitat. While expert opinion can sometimes be predictive (e.g., Murray et al. 2009), other studies suggest that this is not always the case (e.g., Clevenger et al. 2002, Seoane et al. 2005). Two concurrent projects are underway to map high marsh along most of the United States Atlantic Coast and Florida Gulf Coast. Data from these projects may help refine Black Rail habitat models, making identification of potential habitat more effective.

A final consideration around Black Rail detectability is the timing of the surveys. Migrant birds may still be present in April, suggesting that if birds are detected only in that month at a particular site, then that site may not constitute a breeding site. However, we consider this possibility relatively unlikely for our surveys because most of the properties that had detections in April also had at least one or more detections in May or June.

There are several alternative approaches to a traditional occupancy study design that future studies may want to consider. Researchers

monitoring the Sierra Nevada foothills population of California Black Rails have taken a modified occupancy approach in which a wetland is the unit of occupancy (Richmond et al. 2008; S. R. Beissinger, University of California, pers. comm.) but may contain multiple non-independent survey points in close proximity (≥ 50 m). Once a wetland is determined to be occupied, it is no longer surveyed again during that breeding season, akin to a removal sampling design, which is often an efficient approach to surveying species that are difficult to detect (MacKenzie and Royle 2005). Population status is assessed by examining the number of wetlands occupied in a given season, long-term persistence, and trends in extinction and colonization rates. Advantages of this approach are that it allows observers to cover a greater number of sites and gain a clearer picture of metapopulation dynamics. Conversely, it does not allow for any kind of density or population estimation and interpreting the influence of habitat characteristics at the point level becomes more difficult. In Florida's large wetlands, it may be difficult to discretize wetland patches in a biologically meaningful way, whereas the wetlands of the Sierra foothills are naturally well-defined and small.

Another promising alternative is the use of autonomous recording units (ARUs), the use of which is currently being explored by a number of Black Rail researchers. Advantages include the ability to observe for longer periods of time, thus allowing researchers to detect naturally vocalizing individuals (Bobay et al. 2018). The ARUs produce large data files that until recently have required hundreds of hours of staff time to examine, but advances in machine learning approaches to song detection suggest that automatic processing of ARU data via tools such as Cornell University's BirdNet Sound ID (birdnet.cornell.edu) may be an effective and cost-efficient choice for Black Rail researchers (H. Levy, Tall Timbers Research Station and Land Conservancy, pers. comm.). Projects wishing to monitor a large area would need to invest in large numbers of units or have the staff time to move those units frequently, however, as our experience suggests that ARUs have a limited range for recording Black Rails (<150 m). Further development of survey design and protocols is a high priority and an area of active research in the Black Rail conservation community (ACJV 2020), and researchers should consult the most recent literature and organizations focused on Black Rail conservation such as the Atlantic Coast Joint Venture (acjv.org) when designing studies.

Despite the low numbers of Black Rail detections during this study, the broad distribution of the species across the state and persistence at historical sites indicates that Florida is of conservation importance to the Eastern Black Rail. In addition, Florida may support a large number of wintering Black Rails from northern migratory populations. Given

the apparent decline in Eastern Black Rail populations elsewhere, it is important that we continue to rigorously monitor the species and protect and maintain Black Rail habitat in Florida, especially where they currently occur.

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LITERATURE CITED

- ABIY, A. Z., A. M. MELESSE, W. ABTEW, AND D. WHITMAN. 2019. Rainfall trend and variability in Southeast Florida: implications for the freshwater availability in the Everglades. *PLoS ONE* 14:e0212008.
- ACJV [ATLANTIC COAST JOINT VENTURE]. 2020. Eastern Black Rail Conservation Plan for the Atlantic Coast. https://www.acjv.org/documents/BLRA_Plan.pdf. Accessed 19 August 2022.
- BOBAY, L. R., P. J. TAILLIE, AND C. E. MOORMAN. 2018. Use of autonomous recording units increased detection of a secretive marsh bird. *Journal of Field Ornithology* 89:384–392.
- CLEVENGER, A. P., J. WIERZCHOWSKI, B. CHRUSZCZ, AND K. GUNSON. 2002. GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. *Conservation Biology* 16:503–514.
- CONWAY, C. J. 2011. Standardized North American marsh bird monitoring protocols. *Waterbirds* 34:319–346.
- CONWAY, C. J., C. SULZMAN, AND B. E. RAULSTON. 2004. Factors affecting detection probability of California black rails. *Journal of Wildlife Management* 68:360–370.
- EDDLEMAN, W. R., R. E. FLORES, AND M. LEGARE. 2020. Black Rail (*Laterallus jamaicensis*), version 1.0. *in* Birds of the World (A. F. Poole and F. B. Gill, Eds.). Cornell Lab of Ornithology, Ithaca.
- FAIR, J., E. PAUL, AND J. JONES. 2010. Guidelines to the use of wild birds in research. Ornithological Council, Washington, D.C.
- FLORES, R. E., AND W. R. EDDLEMAN. 1995. California black rail use of habitat in southwestern Arizona. *Journal of Wildlife Management* 59:357–363.
- HALL, L. A., N. D. SCHMIDT, AND S. R. BEISSINGER. 2018. Validating dispersal distances inferred from autoregressive occupancy models with genetic parentage assignments. *Journal of Animal Ecology* 87:691–702.

- LEGARE, M. L., AND W. R. EDDLEMAN. 2001. Home range size, nest-site selection and nesting success of black rails in Florida. *Journal of Field Ornithology* 72:170–177.
- LEGARE, M. L., W. R. EDDLEMAN, P. A. BUCKLEY, AND C. KELLY. 1999. The effectiveness of tape playback in estimating black rail density. *Journal of Wildlife Management* 63:116–125.
- MACKENZIE, D. I., AND J. A. ROYLE. 2005. Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology* 42:1105–1114.
- MILLSAP, B. A., J. A. GORE, D. E. RUNDE, AND S. I. CERULEAN. 1990. Setting priorities for the conservation of fish and wildlife species in Florida. *Wildlife Monographs* 111.
- MURRAY, J. V., A. W. GOLDIZEN, R. A. O'LEARY, C. A. MCALPINE, H. P. POSSINGHAM, AND S. LOW CHOY. 2009. How useful is expert opinion for predicting the distribution of a species within and beyond the region of expertise? A case study using brush-tailed rock-wallabies *Petrogale penicillate*. *Journal of Applied Ecology* 46:842–851.
- RICHMOND, O. M., J. TECKLIN, AND S. R. BEISSINGER. 2008. Distribution of California black rails in the Sierra Nevada foothills. *Journal of Field Ornithology* 79:381–390.
- RUNDE, D. E., P. D. SOUTHALL, J. A. HOVIS, R. SULLIVAN, AND R. B. RENKEN. 1990. Recent records and survey methods for the black rail in Florida. *Florida Field Naturalist* 18:33–35.
- SEOANE, J., J. BUSTAMANTE, AND R. DÍAZ-DELGADO. 2005. Effect of expert opinion on the predictive ability of environmental models of bird distribution. *Conservation Biology* 19:512–522.
- TOLLIVER, J. D. M., A. A. MOORE, M. C. GREEN, AND F. W. WECKERLY. 2019. Coastal Texas Black Rail population states and survey effort. *Journal of Wildlife Management* 83:312–324.
- USFWS [U.S. FISH AND WILDLIFE SERVICE]. 2020. Threatened species status for eastern black rail with a Section 4(d) rule. *Federal Register* 85:63764.
- WARD, M., M. JUNTUNEN, D. MITCHELL, AND L. NESTER. 2016. King Rail (*Rallus elegans*) and Black Rail (*Laterallus jamaicensis*) observations in the Florida Everglades. *Florida Field Naturalist* 44:55–59.
- WATTS, B. D. 2016. Status and distribution of the eastern black rail along the Atlantic and Gulf Coasts of North America. The Center for Conservation Biology Technical Report Series, CCBTR-16-09. College of William and Mary/Virginia Commonwealth University, Williamsburg, Virginia.
- WATTS, B. D., D. F. BRINKER, M. D. WILSON, F. M. SMITH, AND C. H. HINES. 2021. Decline of Eastern Black Rails (*Laterallus jamaicensis jamaicensis*) within the Chesapeake Bay Region, USA. *Waterbirds* 44:257–267.
- WILSON, M. D., B. D. WATTS, AND F. M. SMITH. 2009. Status and distribution of black rails in Virginia. Center for Conservation Biology Technical Report Series, CCBTR-0-010. College of William and Mary and Virginia Commonwealth University, Williamsburg, Virginia.

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PATTERNS OF SCAVENGING ON BIRD CARCASSES IN A COASTAL SUBTROPICAL ENVIRONMENT

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Abstract.—There is a need for more information about the mortality of birds using the Atlantic Flyway during migration. One way to evaluate mortality is to monitor the number of carcasses, but bird carcasses are rarely seen in southeast Florida coastal ecosystems, presumably because of a high rate of scavenging. We used infrared automatic game cameras baited with frozen feeder Chickens (*Gallus domesticus*) to assess the scavenging communities in two common southeast Florida coastal subtropical land cover types during the dry (migratory) season: wet intertidal grounds around mangrove roots and dry grounds above the high tide line around trees, coastal shrubs, and grasses. Regardless of individual size, almost all carcasses were removed within 12 hours of being deployed, and all were removed within 24 hours. The three most sighted scavenging species were Virginia opossum (*Didelphis virginiana*), common raccoon (*Procyon lotor*), and marsh rice rat (*Oryzomys palustris*) in both cover types. We observed only one photo of one domestic cat (*Felis catus*) over all the deployments, despite local agency concern about bird predation by large feral cat populations in the region. Because of the high rate of local scavenging and rapidity of removals, observed carcass numbers in natural coastal ecosystems is not recommended as a direct mortality proxy for migratory bird species in southeast Florida.

Key words: scavenging, mangrove, coastal, feral cat

The quantification of mortality rates in wild birds is important for demographic analyses of populations, including the estimation of

anthropogenic effects like wind turbines and pollution. Quantifying mortality through the presence of carcasses has been used for numerous purposes, including oil spills (Fowler and Flint 1997) and wind turbines (Osborn et al. 2000). Historically, one approach to quantifying the mortality of birds during migrations has been to monitor a given area for carcasses (Prosser et al. 2008, Ponce et al. 2010, Kummer et al. 2016). However, this method is sensitive to high rates of scavenging, vegetation coverage, and habitat complexity, which affects the variability in detection success by human observers. Carcass removal by vertebrates is also a complex ecological process affected by many biotic and abiotic factors, and rates of carcass removal are of considerable interest to biologists assessing local avian populations (Antworth et al. 2005). Quantifying avian mortality rates without accounting for these confounding factors can result in underestimates leading to misinformation and inaccurate management decisions (Powers 2021). The Peninsular Florida region has been increasingly subject to human development, providing novel food and habitat resources for numerous medium-sized predatory species that at least partially forage via scavenging, including Eastern spotted skunk (*Spilogale putorius*), Virginia opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), and feral and pet non-native housecats (*Felis catus*; Manaro 1961, Hatley 2002, Klinkowski-Clark et al. 2010, Nicholson and Cove 2022). It is highly likely that scavengers exert an effect on the rates of visible mortality (i.e., observed dead individuals) for birds in the subtropics of southeast Florida, thereby biasing estimates. Direct assessment of scavenging activities could be a solution to this data gap.

Southeast Florida lies along the Atlantic Flyway migratory route and is important for 395 migratory bird species (BirdLife International 2010). Despite its location along the Atlantic Flyway for transient migratory bird species and use as a wintering ground for other species, the southeast Florida region has never been examined for the rates of carcass removals and the activity of scavenging species that would be needed prior to the development of focused surveys to systematically assess bird mortality. This project used baited infrared automatic game cameras to provide first insights on scavenging species and carcass removal for two land cover types in an urban, coastal park intensively used by migratory and resident birds.

METHODS

We conducted this study in West Lake Park in Broward County, Florida. We obtained research permits from the Florida Fish and Wildlife Conservation Commission (LSSC-18-00060) and Broward County (ES2019-001), although university Institutional Animal Care and Use Committee approval was not needed because the research was only observational (S. Tavakoli, Nova Southeastern University, pers. comm.).

We deployed game cameras and baits in two types of land cover that dominate the park area and are commonly found in southeast Florida: 1) wet mud grounds around the roots of red mangrove (*Rhizophora mangle*) and black mangrove (*Avicennia germinans*) trees in the mid to high tide line and 2) dry grounds above the high tide line around native sea grape (*Coccoloba uvifera*) and buttonwood (*Conocarpus erectus*) and invasive Australian pine (*Casuarina equisetifolia*) trees. We set up Moultrie infrared game cameras (models MFH-DGS-D55IR-P [$n = 10$] and MFH-DGS-D55IR [$n = 7$]; Moultrie, Calera, AL, USA) with 5.0 megapixel camera resolution on 15-s intervals between detection and image capture to ensure records of even brief scavenger species interactions with the baits. These camera models have a range of 10.7 m (± 1.5 m). We secured cameras to trees approximately 2–3 m from the bait placements with a slight downward angle (~ 15 – 20 degrees) in locations at least 3 m from any park trail. We reset the internal camera clock prior to each deployment. The first round of camera deployments occurred from January to March 2019, with a second round from October 2019 to January 2020. Both time periods occurred within the dry season of southeast Florida between October and May (Ali et al. 2000). Camera and bait deployments occurred in the morning following sunrise (~ 0800 – 1000 local time; West Lake Park opens to the public at 0800) with camera recoveries approximately 48 hours later, also during morning hours.

We used commercially obtained whole frozen Chicken (*Gallus domesticus*) carcasses (feeder chickens; RodentPro LLC, Evansville, IN, USA) as bait. Carcasses were fully feathered, naturally neutrally colored, and pre-classified by the supplier into four different sizes: extra small (~ 31 – 48 g, $n = 19$ deployments; size simulates small passerines), small (~ 57 – 170 g, $n = 28$; size simulates large passerines), large (~ 284 – 397 g, $n = 28$; size simulates small raptors and gulls), and 3X-large ($\sim 1,500$ – $3,000$ g, $n = 8$; size simulates pelicans). We weighed baits before and after deployments to assess percent consumption. We secured thawed carcasses to bases of trees within view of the game camera using biodegradable sisal twine to prevent movement from tidal water level changes in mangrove emplacements and any scavenger from leaving the field of view with the carcasses before image capture. Blue land crab (*Cardisoma guanhumi*) burrows are ubiquitous throughout the park, but we placed baits >1 m from any observed burrow.

Following deployments, we removed cameras and any remaining bait and downloaded photos from memory cards in the laboratory. For missing bait, we searched a 5-m radius around the deployment site. We considered animals to be scavengers if their heads were next to (<10 cm) and facing the bait; a photo of actual ingestion was not required. We determined time of scavenging from the internal camera timestamp on each photo, with times binned into either within 12 hours of initial deployment or within 24 hours. We did not observe fiddler crab (*Uca* sp.) scavenging directly, likely because their behavior was below the infrared (heat) or size threshold for the game cameras, but carcasses disappeared in intertidal zones interlaced with this species' burrows. Because we did not see any direct interactions, ultimately we did not include the species as a scavenger.

For the purposes of statistical analyses, we combined Black Vulture (*Coragyps atratus*) and Turkey Vulture (*Cathartes aura*) into a single vulture category because of their similar feeding modalities, resulting in six species categories. As comparisons of simple numbers of photos would bias results towards species with long interaction durations with the carcass, we assessed individual scavenger encounters as continuous photos of the same animal, including continuous images separated by less than 10 minutes and showing an animal of a similar size and same species. For analyses, the interaction duration term brief encounter is defined as ≤ 45 seconds (one to three photos) identified to species, whereas an engagement is defined as ≥ 1 minute (at least four continuous photos). We performed two chi-square tests of independence at the level of individual interactions to assess the relationship between the three main scavenging species and 1) land cover types and 2) carcass size ($\alpha = 0.05$).

RESULTS

We made 83 camera deployments within West Lake Park (Fig. 1). The first round of 43 deployments occurred from January through March 2019, but 13 failed to produce images because of camera failures ($n = 7$), theft ($n = 1$), or displacements (camera was knocked out of position; $n = 5$). Out of the 30 successful deployments, 22 resulted in scavenging images. The second round of 40 deployments with padlocked cameras occurred from October 2019 through January 2020. In the second round, 33 yielded images, all containing at least one image of a scavenger. Deployments that did not capture any images during the second round resulted from human tampering ($n = 1$), camera failures ($n = 2$), or camera displacement ($n = 4$).

Scavengers removed carcasses from their tethers and the area immediately around the original deployment site for all but six of the total deployments that yielded images. All the carcasses that were removed were gone within 24 hours, although many (43%) of the carcasses were removed in a shorter time interval of less than 12 hours. We found remains of carcasses on the tether for four deployments that produced images of scavengers but did not have the carcass removed. We estimated the percentage of consumption of these non-removed carcasses at 12% (small carcass, scavenged and buried in a mound by ants), 49% (small carcass, scavenged by ants), 96% (small carcass, scavenged by marsh rice rats [*Oryzomys palustris*]), and 51% (large carcass, scavenged by an unknown organism). Two additional deployments occurred in which the carcass was not fully consumed; scavengers removed the carcasses from the tether and out of view of the camera and we found their remains near the deployment site (within 10 m) with consumption percentages of 89% and 49%. Both carcasses were the 3X-large size and photos documented that they had been scavenged by raccoons.

We observed eight species of animals scavenging on the carcasses, including five vertebrates (raccoon, opossum, marsh rice rat, turkey vulture, black vulture) and two invertebrates (ants and blue land crab). The three mammals dominated the number of photos, and many had more brief encounters than lengthier engagements (Table 1). In contrast, all of the vulture interactions with the baits were the lengthier engagements, with four of the six observations lasting an hour or longer; one observation with a Black Vulture and Turkey Vultures feeding on the same bait carcass lasted 89 minutes. Some species were captured by the game cameras but were not observed to scavenge or even approach the carcasses. These included green iguana (*Iguana iguana*, $n = 4$), knight anole (*Anolis equestris*, $n = 1$), Yellow-Crowned Night Heron (*Nyctanassa violacea*, $n = 2$),



Figure 1. Map displaying the infrared game camera deployment locations in West Lake Park (Broward County, Florida) from scavenging activity trials conducted from January 2019 through January 2020. Land cover types include type 1 (wet mud grounds below high tide line in red and black mangrove), and type 2 (dry grounds above the high tide line). We present successful (full duration with clear view of carcass) and unsuccessful deployments.

Table 1. Scavenger visit durations for the five main species scavenging Chicken carcasses during infrared game camera deployment locations in West Lake Park (Broward County, Florida) from scavenging activity trials conducted from January 2019 through January 2020. The duration term brief encounter is defined as ≤ 45 seconds (one to three photos), whereas engagement is defined as ≥ 1 minute (at least four continuous photos).

Duration	Duration category	Common Raccoon	Virginia Opossum	Marsh Rice Rat	Turkey and Black Vultures	Blue Land Crabs
15 seconds	brief encounter	41	44	26		
30–45 seconds	brief encounter	26	8	5		1
1–15 minutes	engagement	39	22	10		2
16–59 minutes	engagement	18		1	2	
≥ 60 minutes	engagement				4	
Total		124	74	42	6	3

Common Yellowthroat (*Geothlypis trichas*, $n = 1$), eastern grey squirrel (*Sciurus carolinensis*, $n = 3$), and a juvenile White Ibis (*Eudocimus albus*, $n = 1$). We captured one photo of a domestic cat (*Felis catus*) in dry grounds above the high tide line at night, but the orientation of the individual respective to the bait carcass indicated that it was not scavenging. Representative game camera photos of these interacting species are available online as Supplementary Materials (https://nsuworks.nova.edu/occ_facdatasets/15/).

Some of the carcasses had multiple vertebrate scavengers within the camera visual frame within the deployment period, occasionally simultaneously (especially raccoons), but no camera captured more than three different species that interacted over the full deployment duration with a single carcass. There were clear differences between daylight and night scavenging between species (Fig. 2). Turkey Vultures and a Black Vulture were only seen scavenging during daylight hours, with blue land crabs also mostly active during the day (67% of observations). In contrast, marsh rice rats (94.1%) and opossums (96.4%) were almost only seen at night. Common raccoons were mostly active at night ($n = 57$ encounters, 96% night).

Between the two land cover types, three mammal species were most commonly observed scavenging the carcasses: raccoons, opossums, and marsh rice rats. However, the data did not provide evidence of a relationship between scavenger species and land cover type ($\chi^2 = 0.956$, $df = 2$, $n = 90$, $P = 0.9656$). Larger species scavenged on larger carcasses ($\chi^2 = 19.531$, $df = 6$, $n = 123$, $P < 0.001$), driven mostly by opossums and marsh rice rats feeding predominantly on extra small carcasses and raccoons being able to feed on size large and 3X-large chickens (Fig. 3).

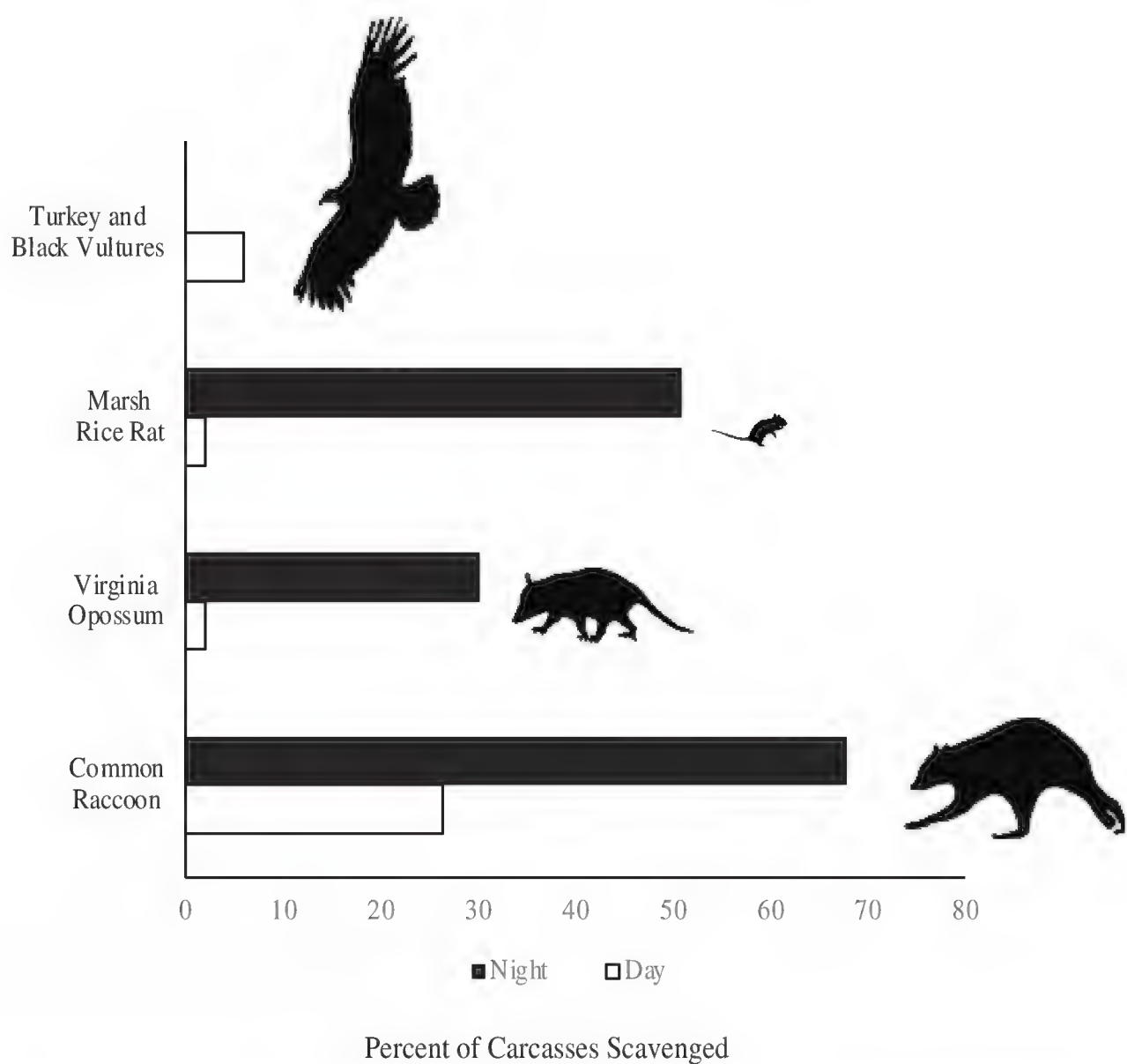


Figure 2. Percent of Chicken carcasses scavenged by photoperiod for vertebrate species recorded during infrared game camera deployment locations in West Lake Park (Broward County, Florida) during trials from January 2019 through January 2020.

DISCUSSION

The camera deployments were focused during the southeast Florida dry season from October through May, which is also the period of highest local numbers for migratory birds. Scavenging may occur even more quickly during the summer wet season with fewer carcasses available from migrants. Many of these scavenging species are also opportunistic predators and prefer the edge habitats typically found in many suburban locations (Wilcove 1985, Small and Hunter 1988). Although Whitcomb et al. (1981) focused on the effects of edge habitats in structuring predation patterns in temperate hardwood forests, similar patch dynamics in edge habitats for scavengers also apply in southeast Florida with scrub pine and mangroves interspersed between housing and commercial developments. Future studies may

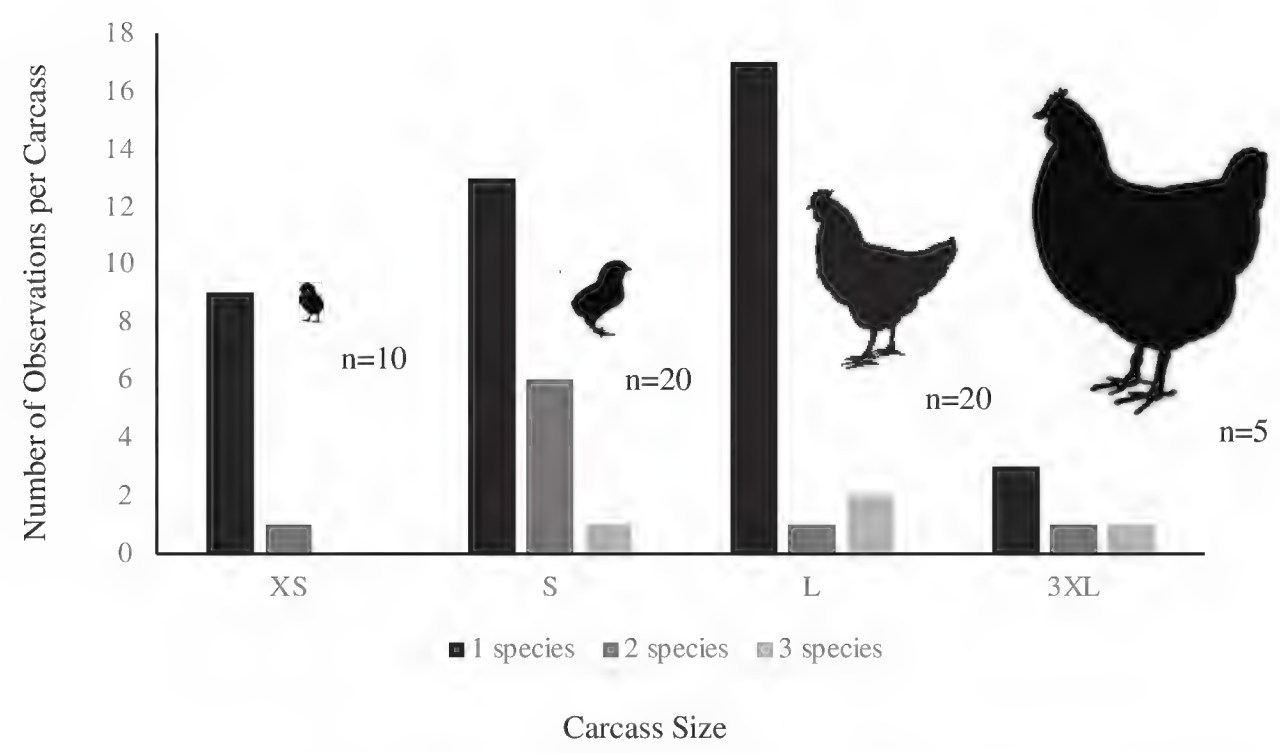


Figure 3. Number of scavenging observations for Chicken carcasses per carcass size and number of combined scavenging species during infrared game camera deployment locations in West Lake Park (Broward County, Florida) from trials conducted from January 2019 through January 2020. Observations include brief interactions and longer duration encounters. Carcasses were naturally neutrally colored and pre-classified by the supplier into four different sizes: extra small (XS), small (S), large (L), and 3X-large (3XL).

wish to explicitly incorporate seasonality into their experimental designs to account for this difference in local bird numbers and how environmental and anthropogenic factors such as land use patterns might affect the behaviors of the scavenging species.

Prior studies using carcass surveys reported scavenging activities occurring within seven days, a lengthy period of time (Prosser et al. 2008, Kummer et al. 2016, Powers 2021). It is unclear whether the higher latitudes of these prior studies perhaps had confounding results regarding scavenger activity, such as winter diapause or adverse weather, which was not an issue in subtropical southeast Florida. In contrast, all the deployed carcasses observed to be scavenged in this present study were removed within 24 hours, with the majority (72%) scavenged over a shorter time span of within 12 hours, a finding similar to Ratton et al. (2014) and Schwartz et al. (2018) with simulated roadkill events in urban areas. Similarly, Antworth et al. (2005) found that 60–97% of bird and snake carcasses on central Florida roadsides disappeared within 36 hours. Because of the speed in which carcasses were removed by scavengers, Schwartz et al. (2018) estimated that the actual number of roadkill deaths may be up to six times higher than observed carcasses. The even shorter period of removals observed

in southeast coastal Florida strongly suggests that migratory bird carcasses (of any size class) are scavenged in a short interval following mortality. These findings also validate Kostecke et al. (2001), which suggested that carcass removal studies check on baits within 24 hours of deployments.

The sensitivity of the cameras did not record fiddler crabs scavenging on the carcasses because of their small size, slow speed, and low vertical profile. Similarly, game camera evidence of other small invertebrates are thus likely an undercount of the total scavenging activities. Ant activity was directly recorded by the game cameras during several instances, but the majority of ant activity was seen incidentally on carcasses being fed upon by larger animals. Such ant scavenging has also been noted in prior carcass removal studies (Griffiths et al. 2017, Clarke et al. 2020) and the reported activity in West Lake Park is likely an undercount of partial, unobserved ant scavenging on other carcasses. More frequent in-person monitoring of the deployed carcasses might have observed additional ant scavenging, but at the potential cost of otherwise disrupting the behaviors of other scavengers. Subsequent studies should also determine the ant species, as few are known to bury carcasses.

The use of infrared automatic game cameras has been used in numerous prior studies of carcass removals (Bauer et al. 2005, Hill et al. 2018) and appeared to be an efficient method of observing and characterizing scavenger presence. Characterizing such scavenging activities can also provide a better estimate of how many carcasses are being removed locally. A higher rate of carcass removal, like the one exhibited in this experiment, suggests that there are likely numerous carcasses not included in mortality surveys and that estimates of mortality could be much higher than projected if simply counting the number of carcasses found in an area. The method of using individual photos as data is potentially confounding because it may bias the results regarding scavenger visit duration. Even since the conclusion of this project in 2020, infrared game cameras have improved significantly in programming options and performance (many are now capable of continuous video, up to 12-megapixel image resolution, and increased memory capacity) while decreasing in price per unit. More frequent and higher resolution images and video would allow for better discrimination between scavengers and allow for better estimates of scavenger visit durations. Although the cameras used in this project were sufficient for species identification and time of contact with the bait, the combination of technological improvements and price reductions should enable future studies to further examine such important aspects as handling of the carcass by the scavenger and the length of time needed to consume or remove the carcass from the field of view to other locations.

Raccoons, opossums, and marsh rice rats, all mammals, were the species with the highest scavenging presence. Mammals are generally some of the more dominant organisms in a food web and require larger amounts of food and energy. Because these scavenging mammals had the largest scavenging presence in the sampling area, it can be inferred that areas with larger populations of these types of organisms are to have higher rates of carcass removal. The rate of incidental anthropogenic provisioning of mesopredators (often scavengers, like raccoons and opossums) can also affect local abundance (Bozek et al. 2007, Theimer et al. 2015). This underlying question of scavenger population size makes it more difficult to provide an accurate estimate of mortality of migratory birds than just surveying animal carcasses. Using scavenger population information to provide an improved estimate of potential scavenging presence would lead to a better characterization of overall scavenging rates and therefore a better characterization of mortality rates.

The study also had some unusual sightings. For example, a Turkey Vulture exhibited semi-aquatic behavior by feeding on a carcass while up to its legs in water (Fig. 4). Many of the camera deployments were in close proximity to blue land crab burrows, but surprisingly only two of them were observed to be feeding on any carcass, despite their description as occasionally eating carrion (Herreid 1963, Hostetler et al. 2019). Perhaps most striking was the near absence of feral or pet domestic cats, with only one sighting (without a visible collar; Fig. 4) in all 83 baited camera deployments. Feral cat populations in southeast Florida remain a contentious public policy problem (Hatley 2002, Robertson 2008), and one of the local state parks declined the use of its non-public areas for this study because of concerns that carcass deployments would attract domestic cats into its restored habitats. Despite the real concern about domestic cats in the coastal southeast Florida ecosystem, these results suggest their main impacts may be from direct predation on birds rather than scavenging carcasses that would otherwise be consumed by native species.

The coastal environments of southeast Florida along the Atlantic Flyway are the locations of some level of mortality on migratory birds, including direct predation and incidental mortalities from such sources as building strikes. Implicit in some literature was the assumption that smaller bird carcasses were more likely to be removed quickly, but even large-bodied carcasses in this study were scavenged and removed quickly in the two assessed land cover types, often interacting with multiple scavenging species on the same deployment. Scavenging also occurred during both day and night periods, although mostly at night. Future studies should more rigorously assess the role of carcass size in removal rates, and consider standardized survey methodologies, a



Figure 4. Encounter of Turkey Vulture feeding in shallow tidal saltwater in wet mud grounds in mangroves during the day while feeding on a large Chicken carcass (22 Jan 2020; top). The original photo is in color, showing the red coloration of skin on the head (available in the online Supplemental Materials at https://nsuworks.nova.edu/occ_facdatasets/15/). Interaction of domestic cat in dry grounds above the high tide line at night (9 Mar 2019; bottom). A tethered Chicken carcass is behind the cat; however, we did not consider this single photo of the cat to be indicative of scavenging on the Chicken carcass bait.

point emphasized by Loss et al. (2012). Regardless of land cover type, the short duration of carcasses on the ground shown in this study in subtropical southeast Florida indicates that agencies and other organizations should use surveys of dead birds as a proxy of migration-related mortality only with extreme caution.

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LITERATURE CITED

- ALI, A., W. ABTEW, S. VAN HORN, AND N. KHANAL. 2000. Temporal and spatial characterization of rainfall over Central and South Florida. *JAWRA Journal of the American Water Resources Association* 36:833–848.
- ANTWORTH, R. L., D. A. PIKE, AND E. E. STEVENS. 2005. Hit and run: effects of scavenging on estimates of roadkilled vertebrates. *Southeastern Naturalist* 4:647–656.
- BAUER, J. W., K. A. LOGAN, L. L. SWEANOR, AND W. M. BOYCE. 2005. Scavenging behavior in puma. *Southwestern Naturalist* 50:466–471.
- BIRDLIFE INTERNATIONAL. 2010. Atlantic Americas Flyway. http://datazone.birdlife.org/userfiles/file/sowb/flyways/3_Atlantic_Americas_Factsheet.pdf. Accessed 14 July 2022.
- BOZEK, C. K., S. PRANGE, AND S. D. GEHRT. 2007. The influence of anthropogenic resources on multi-scale habitat selection by raccoons. *Urban Ecosystems* 10:413–425.
- CLARKE, M. J., E. E. FRASER, AND I. G. WARKENTIN. 2020. Fine spatial-scale variation in scavenger activity influences avian mortality assessments on a boreal island. *PLoS One* 15:e0233427.
- FOWLER, A. C., AND P. L. FLINT. 1997. Persistence rates and detection probabilities of oiled king eider carcasses on St Paul Island, Alaska. *Marine Pollution Bulletin* 34:522–526.
- GRIFFITHS, H. M., L. A. ASHTON, A. E. WALKER, F. HASAN, T. A. EVANS, P. EGGLETON, AND C. L. PARR. 2017. Ants are the major agents of resource removal from tropical rainforests. *Journal of Animal Ecology* 87:293–300.
- HATLEY, P. J. 2002. Feral cat colonies in Florida: the fur and feathers are flying. *Journal of Land Use and Environmental Law* 18:441.
- HERREID, C. F. 1963. Observations on the feeding behavior of *Cardisoma guanhumi* (Latreille) in southern Florida. *Crustaceana* 5:176–180.
- HILL, J. E., T. L. DEVAULT, J. C. BEASLEY, O. E. RHODES, AND J. L. BELANT. 2018. Roads do not increase carrion use by a vertebrate scavenging community. *Scientific Reports* 8:1–10.
- HOSTETLER, M. E., F. J. MAZZOTTI, AND A. K. TAYLOR. 2019. Blue land crab (*Cardisoma guanhumi*). Department of Wildlife Ecology and Conservation, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida, Gainesville.

- KLINKOWSKI-CLARK, C., M. J. KUTILEK, J. O. MATSON, P. MESSINA, K. EARLEY, AND S. M. BROSEEMANN. 2010. Estimating relative distribution of raccoons, opossums, skunks, and foxes using animal control data. *Human–Wildlife Interactions* 4:32–46.
- KOSTECKE, R. M., G. M. LINZ, AND W. J. BLEIER. 2001. Survival of avian carcasses and photographic evidence of predators and scavengers. *Journal of Field Ornithology* 72:439–447.
- KUMMER, J., C. NORDELL, T. BERRY, C. COLLINS, C. TSE, AND E. BAYNE. 2016. Use of bird carcass removals by urban scavengers to adjust bird-window collision estimates. *Avian Conservation and Ecology* 11(2):12.
- LOSS, S. R., T. WILL, AND P. P. MARRA. 2012. Direct human caused mortality of birds: improving quantification of magnitude and assessment of population impact. *Frontiers in Ecology and the Environment* 10:357–364.
- MANARO, A. J. 1961. Observations on the behavior of the spotted skunk in Florida. *Quarterly Journal of the Florida Academy of Sciences* 24:59–63.
- NICHOLSON, M., AND M. V. COVE. 2022. Stable isotopes point to anthropogenic subsidies in northern raccoons at the urban-wild interface. *Food Webs* 31:e00233.
- OSBORN, R. G., K. F. HIGGINS, R. E. USGAARD, C. D. DIETER, AND R. D. NEIGER. 2000. Bird mortality associated with wind turbines at the Buffalo Ridge Wind Resource Area, Minnesota. *American Midland Naturalist* 143:41–52.
- PONCE, C., J. C. ALONSO, G. ARGANDOÑA, A. GARCÍA FERNÁNDEZ, AND M. CARRASCO. 2010. Carcass removal by scavengers and search accuracy affect bird mortality estimates at power lines. *Animal Conservation* 13:603–612.
- POWERS, K. E., L. A. BURROUGHS, N. I. HARRIS III, AND R. C. HARRIS. 2021. Biases in bird-window collisions: a focus on scavengers and detection rates by observers. *Southeastern Naturalist* 20:293–307.
- PROSSER, P., C. NATTRASS, AND C. PROSSER. 2008. Rate of removal of bird carcasses in arable farmland by predators and scavengers. *Ecotoxicology and Environmental Safety* 71:601–608.
- RATTON, P., H. SECCO, AND C. A. DA ROSA. 2014. Carcass permanency time and its implications to the roadkill data. *European Journal of Wildlife Research* 60:543–546.
- ROBERTSON, S. A. 2008. A review of feral cat control. *Journal of Feline Medicine and Surgery* 10:366–375.
- SCHWARTZ, A. L., H. F. WILLIAMS, E. CHADWICK, R. J. THOMAS, AND S. E. PERKINS. 2018. Roadkill scavenging behaviour in an urban environment. *Journal of Urban Ecology* 4:juy006.
- SMALL, M. F., AND M. L. HUNTER. 1988. Forest fragmentation and avian nest predation in forested landscapes. *Oecologia* 76:62–64.
- THEIMER, T. C., A. C. CLAYTON, A. MARTINEZ, D. L. PETERSON, AND D. L. BERGMAN. 2015. Visitation rate and behavior of urban mesocarnivores differs in the presence of two common anthropogenic food sources. *Urban Ecosystems* 18:895–906.
- WHITCOMB, R. F., C. S. ROBBINS, J. F. LYNCH, B. L. WHITCOMB, M. K. KLIMKIEWICZ, AND D. BYSTRAK. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125–205 *in* Forest island dynamics in man-dominated landscapes (R. L. Burgess, and D. M. Sharpe, Eds.). Springer-Verlag, New York, New York, USA.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211–1214.

**BLACK SPINY-TAILED IGUANA (*Ctenosaura similis*)
USE OF GOPHER TORTOISE (*Gopherus polyphemus*)
BURROWS IN BUCKINGHAM, FLORIDA**

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Abstract.—Black spiny-tailed iguanas (*Ctenosaura similis*) were introduced to Florida in 1979. Since then, they have become established in several areas and may be a threat to gopher tortoises (*Gopherus polyphemus*), potentially displacing tortoises from their burrows and depredating tortoise eggs. We monitored gopher tortoise burrows that varied in size, orientation, and canopy coverage to document their use by tortoises and iguanas at a site in Lee County, Florida. By setting up trail cameras on 24 burrows, we showed that few (2/24) burrows were regularly occupied by iguanas and documented iguana–tortoise interactions in detail at a single burrow. We found that gopher tortoise burrow locations have higher than average canopy cover and that all burrows with signs of use by iguanas were ≥ 22 cm with canopies $< 26\%$ closed. We observed at least two iguanas and one tortoise sharing a single burrow simultaneously, and at least five different iguanas and one tortoise using the same burrow over a span of at least 7 months. We documented modification of two burrows by iguanas. Additional monitoring of iguana populations is recommended to better understand their impact on gopher tortoises.

Keywords: burrow sharing, cameras, canopy cover, competition, inter-specific interactions, invasive species.

Gopher tortoises (*Gopherus polyphemus*) are a keystone species native to the southeastern United States. They share their burrows with many native vertebrate and invertebrate species (Dziadzio and Smith 2016, Hipps 2019), some of which rely on tortoise burrows for survival. Gopher tortoises are threatened primarily because of habitat loss and degradation (Mushinsky et al. 2006, Ashton and Ashton 2008) but potentially also because of interactions with certain non-native species. For example, red imported fire ants (*Solenopsis invicta*) can kill hatchlings (Epperson and Heise 2003) and reduce the diversity and abundance of commensal invertebrates (Epperson et al. 2020). Other non-native species that have been found in gopher tortoise burrows include longhorn crazy ants (*Paratrechina longicornis*), little fire ants

(*Wasmannia auropunctata*), Emery's sneaking ants (*Cardiocondyla emeryi*; Hipps 2019), greenhouse frogs (*Eleutherodactylus planirostris*; Lips 1991, Witz et al. 1991), domestic cats (*Felis catus*; Melanson 2021), nine-banded armadillos (*Dasypus novemcinctus*; Guyer and Hermann 1997), red-footed tortoises (*Chelonoidis carbonarius*; Melanson 2021), Burmese pythons (*Python bivittatus*; Metzger 2013, Bartoszek et al. 2018, Hengstebeck 2018), Argentine black-and-white tegus (*Salvator merianae*; Engeman et al. 2011), brown anoles (*Anolis sagrei*; Hengstebeck 2018, Hipps 2019), brown basilisks (*Basiliscus vittatus*; Melanson 2021), northern curly-tailed lizards (*Leiocephalus carinatus*; Moore et al. 2017, Melanson 2021), green iguanas (*Iguana iguana*; Truglio et al. 2008, Melanson 2021), and black spiny-tailed iguanas (*Ctenosaura similis*; Engeman et al. 2009). Although gopher tortoises are generally tolerant of native vertebrates that share their burrows, relatively little is known about interactions between non-native species and gopher tortoises.

Black spiny-tailed iguanas are native to the lowlands of Central America from central Panama to southern Mexico (Fitch and Hackforth-Jones 1983), where they either dig burrows or use natural rock crevices or spaces under buildings for nighttime shelter, thermoregulation, and predator avoidance (Fitch and Henderson 1978, Burger and Gochfeld 1991). Preferred burrow locations in Costa Rica have more open canopies than surrounding areas (Burger and Gochfeld 1991). Starting in the late 1970s to early 1980s, black spiny-tailed iguanas were introduced to both Key Biscayne and Gasparilla Island, with a subsequent independent introduction on Keewaydin Island in 1995 (Naccarato et al. 2015, Nuñez 2016). They spread to other Gulf Coast barrier islands throughout the 1990s and 2000s (Krysko et al. 2003). Several populations were initially misidentified as Mexican spiny-tailed iguanas (*Ctenosaura pectinata*; Townsend et al. 2003). They are now found on the mainland from Venice to Port Charlotte, with scattered records south to Marco Island (Krysko et al. 2019, EDDMapS 2023). Black spiny-tailed iguanas do not appear to reach the densities of green iguanas in many parts of Florida, but their large clutch sizes (up to 88; Fitch and Hackforth-Jones 1983, Krysko et al. 2003, Avery et al. 2014) probably allow their populations to grow quickly, especially in the absence of mesopredators. Although they are largely herbivorous (Krysko et al. 2009), one record of predation by a black spiny-tailed iguana on a juvenile gopher tortoise has been documented (Avery et al. 2009). Modifications made by iguanas to gopher tortoise burrows include side channels and second entrances (McKercher 2001, McKnight et al. 2022), and extensive use of gopher tortoise burrows by black spiny-tailed iguanas has been suggested to repel tortoises (Engeman et al. 2009).

Black spiny-tailed iguanas (hereafter iguanas) have been suggested to be a threat to gopher tortoises, potentially by displacing tortoises from their burrows, excavating tortoise nests during burrow modification, and directly consuming tortoise eggs and juveniles (McKercher 2001, Avery et al. 2009, Engeman et al. 2009, Krysko et al. 2009, Avery et al. 2014), although little direct evidence for these claims exists. We monitored 69 gopher tortoise burrows (hereafter, tortoise burrows) at a site in Lee County, Florida. Within our overall goal of collecting as much information as possible about the potential interaction between these two species, our specific objectives were to 1) document any use of tortoise burrows by iguanas, 2) test whether three tortoise burrow characteristics—canopy coverage, size, and orientation—had an impact on use by iguanas, and 3) describe iguana–tortoise interactions at burrows in detail.

METHODS

Study site.—Florida Gulf Coast University’s (FGCU) Buckingham Complex (Fig. 1) is a 200-ha plot of land in Lee County, Florida (26.65509°N, –81.73902°E; WGS84), which was acquired by the university in 2010 after serving as a state-run residential facility for people with developmental disabilities since the late 1950s. About 60% of the property previously served as a self-sustained community with 60 structures, including homes, a gymnasium, and a church, surrounded by mowed lawns. The other 40% is comparatively heavily vegetated slash pine (*Pinus elliottii*) flatwoods (Abrahamson and Hartnett 1990) with a maintained trail system, and an understory of saw palmetto (*Serenoa repens*), Brazilian pepper (*Schinus terebinthifolia*), and about 100 species of native and non-native herbaceous plants and grasses (see list in supplementary material on figshare; DOI: 10.6084/m9.figshare.24021423). Prescribed fire has not been used on the site since at least 2010, but one small lightning fire was ignited in the 2010s. Canals run along the



Figure 1. Map of Florida Gulf Coast University’s Buckingham Complex, Lee County, Florida, with 69 gopher tortoise burrows shown, 2020–2021.

northern and southern border of the property, flowing into the Orange River to the east. Current land use includes recreational sports, law enforcement training, and forensic and ecological research. A population of gopher tortoises has occupied the property for at least 50 years. Iguanas occupied the site at least as early as 2010 but possibly as far back as the 1980s, although the exact origin and date of establishment of this population is unknown. Local contacts have suggested that a hurricane in the late 1980s or very early 1990s, which destroyed an exotic pet store about 1.6 km to the north, was the source of the population.

Burrow surveys.—We located tortoise burrows by conducting 250-m reconnaissance surveys covering about 50% of the site, targeting well-drained, higher elevation potential tortoise habitat. We surveyed for 2–3 hours per day on 35 days between September 2020 and May 2021. We followed existing paths and natural boundaries such as fence lines. We chose a reconnaissance survey because this survey style did not require us to follow straight lines, rather to follow the path of least resistance, which is useful when surveying wildlife in heterogeneous habitats (Walsh and White 1999, Cronin et al. 2016). Some areas were inaccessible due to dense vegetation or had fences, buildings, or other structures that we could not walk around, so this survey style gave us the flexibility to walk as close to a straight-line transect as possible. While walking between burrows during monitoring, we also noted any iguanas that were unrelated to burrows. We recorded each tortoise burrow through the Avenza app (<https://www.avenza.com/>) using sequential numbers. The Avenza app allowed us to mark the exact global positioning system (GPS) location of each tortoise burrow on a georeferenced map and add multiple photographs and notes to each marked burrow. We measured burrow width, orientation, and canopy coverage for each burrow (see below) and recorded these as part of the Avenza app record for the corresponding burrow. We also recorded any signs of use by iguanas, such as footprints, tail drags, or non-tortoise excavation. At any point when we revisited burrows (e.g., to set or check cameras), we also made note of any modifications to burrows and any new burrows that had been excavated nearby through the Avenza app.

We measured the width of the widest point of the mouth of each burrow, in centimeters, using a measuring tape. To measure orientation, we stood as close to the mouth of the burrow as possible without disturbing the substrate surrounding the burrow or the tortoises and placed a compass centered above the opening of each burrow. This allowed us to determine the cardinal direction the opening of each burrow was facing to the nearest degree.

We recorded canopy coverage for each burrow using a spherical densiometer (Forest Densiometer Model A; Forestry Suppliers, Jackson, MS, USA). We measured all recorded canopy coverage at the closest point to the mouth of the burrow. To make the canopy coverage data as consistent as possible, only one researcher (JR) recorded the canopy coverage. To establish if there was a difference in canopy coverage between burrow locations and areas not occupied by burrows, we also took measurements of canopy coverage by choosing a random direction from each tortoise burrow using the RANDBETWEEN function in Excel (Microsoft, Redmond, WA, USA) to generate a number between 1 and 360 for each burrow, corresponding to a cardinal point on a compass. Tortoises tend to only forage within 30 m of their burrow (McRae et al. 1981) so we walked 30 m in the given random direction and took the canopy coverage of that location. We compared canopy coverage from each burrow and of the random point using a paired t-test in R. We also noticed iguanas using man-made structures (e.g., gutters, crevices) and recorded canopy coverage of spots where we frequently observed iguanas.

Trail cameras.—We set up three to four trail cameras at a time between 4 November 2020 and 15 May 2021. We set cameras facing the opening of burrows ($n = 24$) to capture any potential activity of gopher tortoises, iguanas, and other animals. We used Browning StrikeForce BTC-5HD-APX cameras (Browning Trail Cameras, Birmingham, AL, USA) on Trail Mode with a capture delay of 10 seconds and a multi-shot setting of 3 shots.

After four days, we replaced the memory card within each camera and moved the trail cameras to different burrows. We continued to check all tortoise burrows throughout the study, but we did not film all burrows with trail cameras. We selected burrows for filming mostly haphazardly, except that we made sure to include all burrows that had evidence of iguana use. We manually sorted through all photos and recorded all animals, including animals walking or flying across the frame. When iguanas and tortoises were both visible, we also looked for photographic evidence of direct interactions between them. Whenever an animal was captured in a photo, we recorded the species (if possible), burrow number, date, camera number and memory card number. If an animal was repeatedly shown on multiple consecutive frames, we counted these as a single detection event.

Behavior at actively shared burrows.—We documented only one burrow that was actively shared by the two species. To document their interactions in greater detail, we recorded the start and stop time of all iguana and tortoise behavior photographed over the four-day period during 11–14 April 2021. Because of the temporal resolution of the camera settings, we defined the minimum duration of any behavior as 1 minute. We categorized behaviors as basking, walking, drinking, entering burrow, emerging from burrow, or digging. During basking the animal was sitting still in the sun for >1 minute (42 unique events for iguanas, 0 for tortoises; Fig. 2A). We recorded walking behavior when the animal was moving through the frame without interacting with the burrow in any obvious way (15 unique events for iguanas, 3 for tortoises). Drinking indicated the animal was active in the rain (0 unique events for iguanas, 1 for tortoises; Fig. 2B). We recorded entering the burrow when the animal was moving and disappeared into the burrow mouth (10 unique events for iguanas, 3 for tortoises; Fig. 2C). We assigned emerging from the burrow when the animal appeared from within the burrow (12 unique



Figure 2. Captures from Browning StrikeForce BTC-5HD-APX cameras set at the only burrow that was actively shared by gopher tortoises and black spiny-tailed iguanas in Lee County, Florida, 2021. A) One iguana basks on the apron, another on the pipe, while a black racer passes by. B) A tortoise drinks in the rain. C) One iguana enters the burrow as a tortoise sits in the entrance; a second iguana basks on the pipe. D) An iguana digging in the mouth of the burrow; a second iguana basks on the pipe.

events for iguanas, 6 for tortoises). We identified digging behavior when the animal was using its limbs to throw sand (9 unique events for iguanas, 6 for tortoises; Fig. 2D).

We also recorded whether activity took place at or near the burrow apron or away from the apron, mostly because there was a large pipe in the background on which iguanas frequently basked. When more than one individual was engaged in the same behavior, we recorded the number of individuals. We attempted to keep track of individual identity. Sunrise on these four days was at approximately 0705 and sunset was at approximately 1951, giving an average of 766 minutes of daylight.

Data visualization and analysis.—We tested whether three tortoise burrow characteristics—size, canopy coverage, and orientation—had an impact on use by iguanas. We used unpaired t-tests to compare the size and canopy coverage of burrows where we detected iguanas and those where we did not. We compared canopy coverage between tortoise burrows and random points using a paired t-test. We used Watson's two-sample test of homogeneity, also known as Watson's U^2 test (Lund et al. 2001), a circular statistic with high power (Landler et al. 2021), to test for differences in orientation between burrows where we detected iguanas and those where we did not. We used Pearson's χ^2 and Fisher's exact tests on contingency tables of orientation and canopy coverage to test for relationships between these two variables. We carried out all statistical tests in R (R Core Team 2023) using packages ggplot2 (Wickham 2009) and fmsb (Nakazawa 2023) for visualization.

RESULTS

Burrow survey results.—Over the span of 7 months, we documented 69 tortoise burrows. Three of these burrows were newly excavated during the period of our data collection. We could not measure canopy coverage, width, or orientation for 4 of the 69 burrows because they were not accessible, so we did not include these burrows in any analysis. The majority of the burrows bordered the fence running along the western side of the property and separating the wooded trails from the open grassy field (Fig. 1).

We documented iguanas using five different tortoise burrows, three of which were also occupied by a tortoise (Fig. 3). We documented iguana use of two burrows through trail camera, two burrows through direct observation, and one burrow through presence of tail drags (burrow was filmed but no iguanas were photographed). Of the two burrows with direct observations, both burrows were subsequently filmed but iguanas did not appear in the photos; one of these could have been a temporary refuge because the iguana seemed to move into it in order to avoid us. Outside of our burrow surveys and trail camera footage, we observed four iguanas using crevices or gutters in concrete buildings, all of which had 48–49% canopy coverage from roofs of the buildings but were located within a few meters of open areas for basking.

Burrow characteristics.—The average ($\pm$ SD) burrow width for the 65 burrows was 25.6 ($\pm$ 8.1) cm with the smallest burrow width being 5 cm and largest burrow width being 40 cm (Fig. 3). All five burrows with signs of use by iguanas were ≥ 22 cm in width. Burrows with an iguana sighting ($n = 5$) measured an average of 29.8 ($\pm$ 4.7) cm (min = 22 cm,

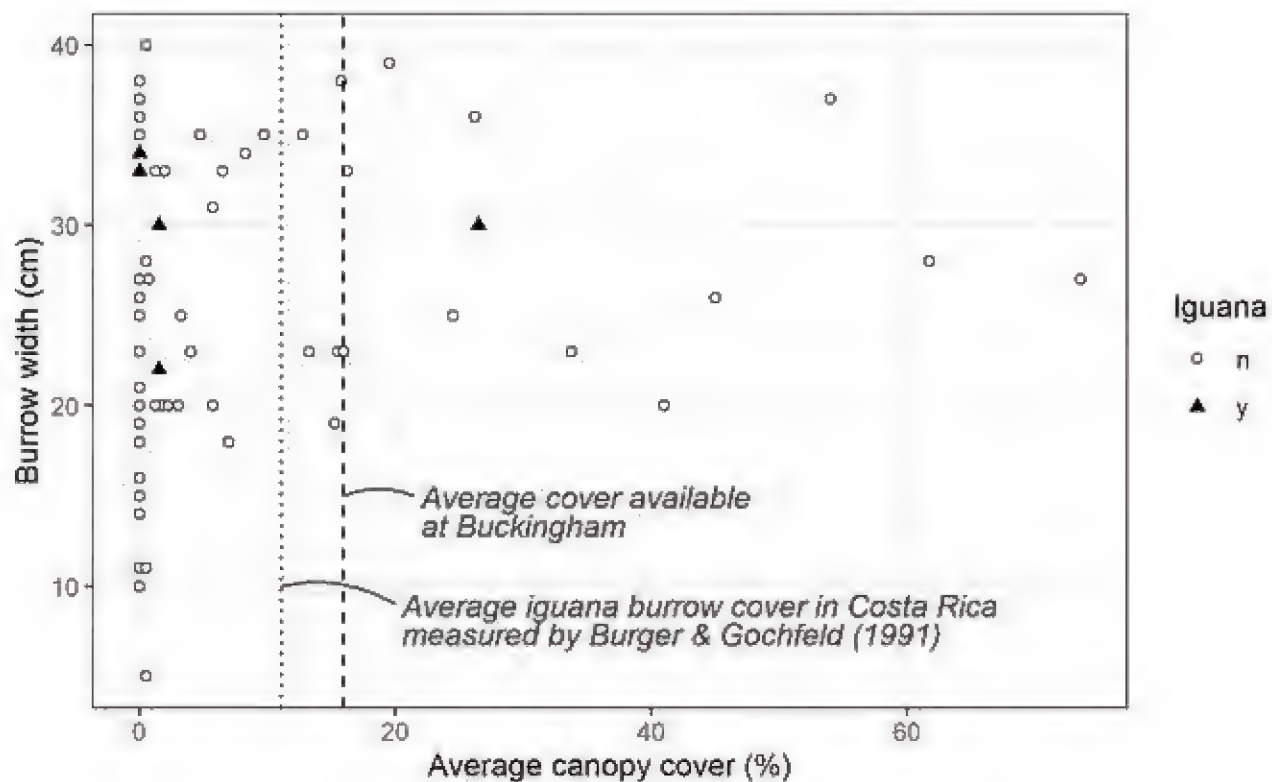


Figure 3. Relationship between average canopy cover and gopher tortoise burrow size (cm) at Florida Gulf Coast University’s Buckingham Complex in 2020, Lee County, Florida. Burrows with iguana presence are filled triangles, those where we did not document iguanas are hollow circles.

max = 34 cm), although we did not find evidence for a difference in size between burrows used by iguanas and those not used by iguanas ($t = 1.95$, $df = 6.25$, $P = 0.097$).

Burrow orientation varied. About one third of burrows (36%) faced north ($315\text{--}45^\circ$), another third (31%) faced west ($225\text{--}315^\circ$), 18% faced south ($135\text{--}225^\circ$), and 14% faced east ($45\text{--}135^\circ$). We did not find evidence for directionality of burrow orientation (null hypothesis = equal number of burrows facing all directions; Pearson’s $\chi^2_{15} = 7.58$, $P = 0.94$; Fisher’s exact test $P = 0.95$). There was no relationship between burrow size and orientation ($F_{1,63} = 0.05$, $P = 0.82$, $R^2 = -0.02$). Of the five burrows used by iguanas, three faced west-southwest, one faced east, and one faced north (Fig. 4). Watson’s two-sample test of homogeneity did not suggest any difference in orientation between burrows used by iguanas and those that were not (test statistic = 0.0994; $P > 0.10$).

We found that tortoise burrows were located in areas with a canopy more open than random (Fig. 5; $t = -2.43$, $df = 64$, $P = 0.02$); median canopy cover above burrows was about 1%, whereas it was about 7% for random points. When we divided burrows into those with canopy coverage below or above the median value of 1.25%, we found that many more burrows with more closed canopies ($>1.25\%$ canopy coverage) faced north, whereas many more burrows with more open canopies ($<1.25\%$) faced west-southwest (Fig. 4). However, there was no

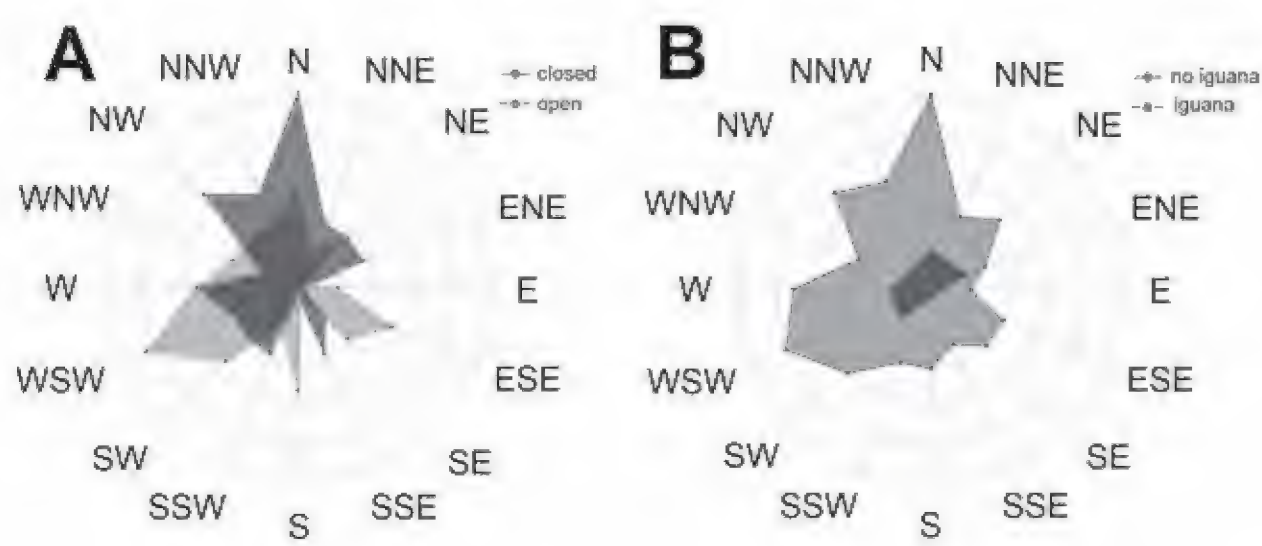


Figure 4. A) Compass orientation of gopher tortoise burrows with canopy coverage above the median value of 1.25% (closed; solid line) and below the median value of 1.25% (open; dashed line) for burrows in Lee County, Florida, 2020–2021. B) Canopy coverage of burrows occupied by black spiny-tailed iguanas (dashed line) and where we did not detect iguanas (solid line).

significant difference between these two groups (Pearson’s $\chi^2_3 = 3.40$, $P = 0.33$; Fisher’s exact test $P = 0.35$). The mean canopy cover at burrows used by iguanas (5.9%) was a little lower than that at burrows not used by iguanas (9.2%), although this difference was not statistically

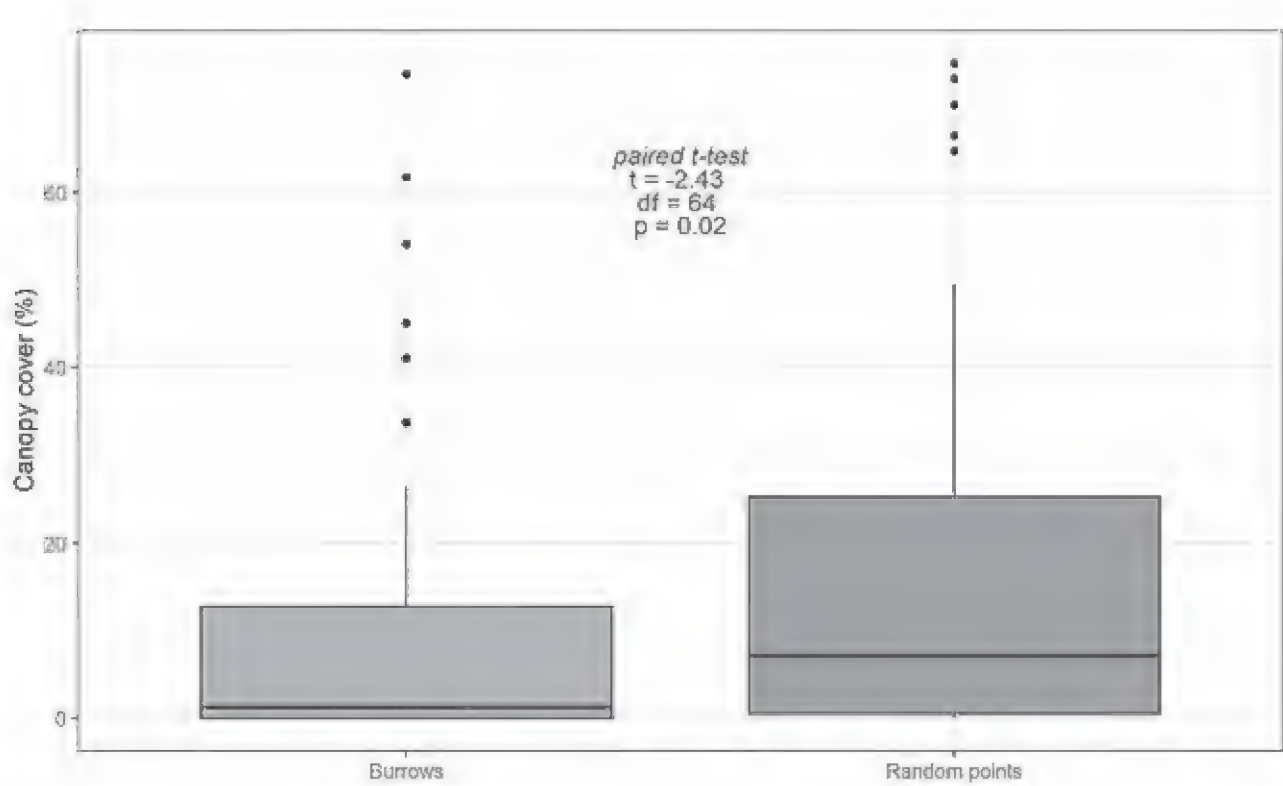


Figure 5. Difference in canopy cover between gopher tortoise burrows and random points 30 m distant at Florida Gulf Coast University’s Buckingham Complex in Lee County, Florida, 2020–2021.

significant ($t = -0.60$, $df = 5.4$, $P = 0.56$). The highest canopy cover at any burrow was 73.5%, whereas the highest canopy cover at a burrow occupied by an iguana was 26.5%.

Trail camera results.—Trail cameras collected a total of 39,062 photos. Data presented here are from a subset of 18 burrows out of 24 monitored. The cameras at the six burrows not presented either did not detect animals or malfunctioned. Out of the total photos collected, only 1,127 (2.9%) captured photos of animals. Tortoises were the most frequently observed species (Fig. 6). We found that hogs were the second most frequently observed but they were never observed interacting with burrows. Iguanas were photographed using two different tortoise burrows, only one of which was in use by a tortoise (Fig. 7). Snakes (black racers [*Coluber constrictor*] and coachwhips [*Masticophis flagellum*]) and fox squirrels (*Sciurus niger*) were photographed using tortoise burrows while there was a tortoise present (Fig. 7). We did not document any evidence of predation or other threats from iguanas to the tortoises or any other animal.

Out of 18 burrows with usable camera data, two of the five burrows used by iguanas were not obviously occupied by tortoises, including one that had been highly modified (presumably by an iguana). Nine burrows were occupied by tortoises with no iguanas photographed, and four burrows had neither tortoises nor iguanas. We documented potential burrow modification by iguanas of at least two burrows; we photographed both a tortoise and an iguana excavating at one burrow (see detailed account below), and the entrance to another burrow had been enlarged, the shape of the entrance changed, and the burrow

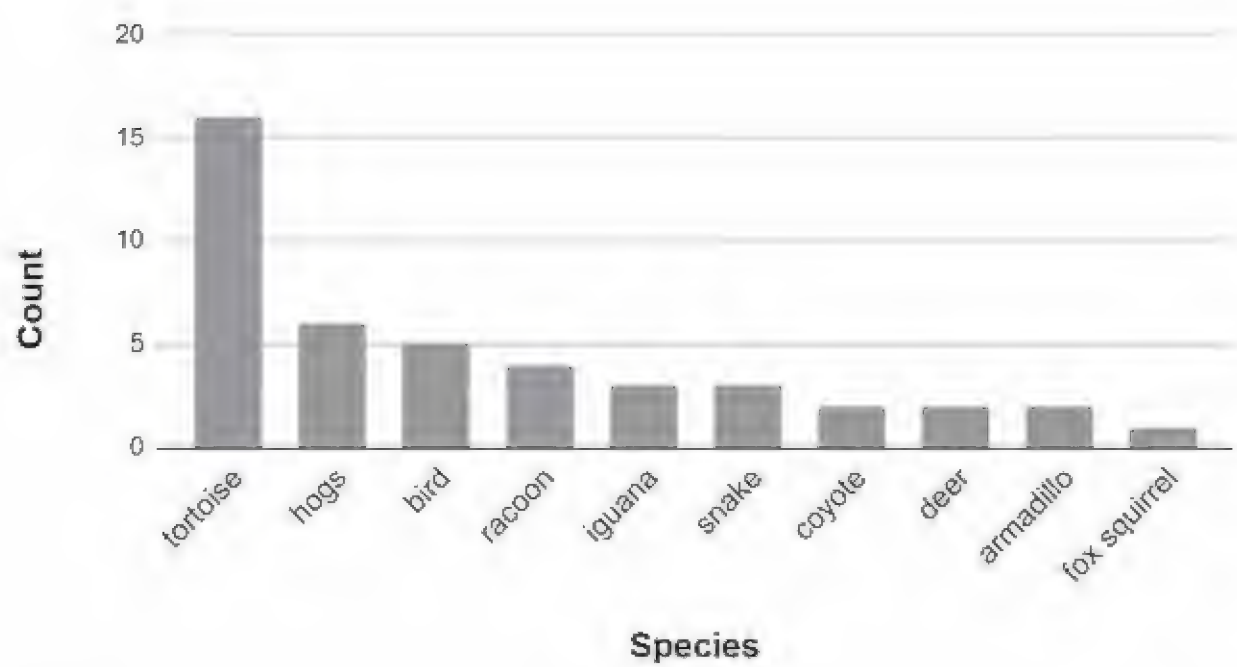


Figure 6. Frequency of all taxa documented at gopher tortoise burrows by trail cameras at Florida Gulf Coast University’s Buckingham Complex in Lee County, Florida, 2020–2021.

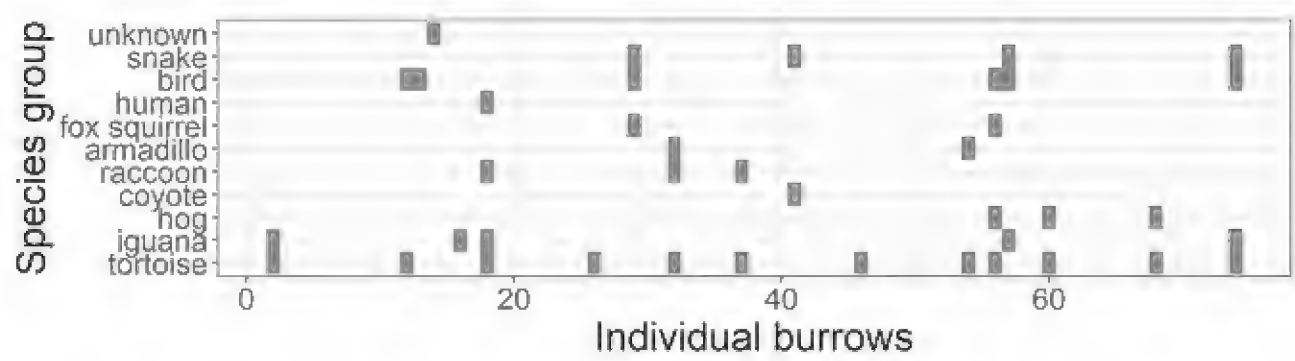


Figure 7. Matrix of species presence on trail camera photos and from direct observation at each gopher tortoise burrow (sequential numbers on *x*-axis), showing burrow sharing by tortoises (bottom row) and iguanas (second from bottom) at three of 69 burrows in Lee County, Florida, 2020–2021.

partially collapsed. We do not know to what extent this could have been due to erosion, possibly exacerbated by a fence post immediately adjacent to the burrow entrance.

Behavior at actively shared burrow.—At least two different iguanas, both females, visited the burrow over the four-day period. It was difficult to assess whether the tortoise in the photographs was always the same individual; no two images showed two tortoises of obviously different size classes so it easily could have been a single individual. A more complete description of the behaviors recorded is provided on figshare (DOI: 10.6084/m9.figshare.24021420).

Iguanas spent between 96 and 230 minutes per day basking (13–30% of the day) in a location that was visible to the camera. On one day (14 April), iguana basking time was split evenly between the burrow apron and the pipe; on the other days, it was skewed heavily toward the pipe (3.8:1 on 12 April; 4.1:1 on 13 April) or the apron (1:5.1 on 11 April). On the afternoon of 11 April there was a rainstorm starting at 1450 (Fig. 2B); no photos were taken after 1459. The weather on the other days was partly to mostly sunny, with no rain.

Iguanas spent almost all of their time basking (91%), with a small amount of time spent walking (4%), entering or exiting the burrow (4%), or digging in the burrow mouth (2%). We observed digging on all three days following the rain storm—twice by a tortoise on 12 April, four times by a tortoise and eight by an iguana on 13 April, and once by a different iguana on 14 April (Fig. 2D).

Iguanas were active at the burrow apron for nearly 7.5 as much time as tortoises over the four-day interval (374 minutes vs. 51 minutes). Tortoises were never observed basking at the burrow apron but spent their time in front of the camera (total of 51 minutes over the four-day period) walking around the burrow entrance (35%), digging in the burrow mouth (28%), entering or exiting the burrow (25%), or drinking during the rainstorm (12%).

The most extensive period of digging by an iguana took place at intervals between 1515 and 1719 on 13 April 2021 (Fig. 2D; <https://imgflip.com/gif/5wrros>). The same iguana dug and threw sand into view of the camera at least 10 times over the two-hour period, interspersed by going deeper into the burrow, returning to the apron, or leaving the burrow entirely for 1–43 minutes between each period of digging. The 10-second capture delay likely prevented us from accurately counting the number of sand throws, and we would not have been able to capture any digging behavior by either species that did not result in at least some sand being thrown within view of the camera, triggering it to take a set of photos. The tortoise was in the burrow during this time period; it poked its head out once at 1641, coming nose-to-nose with a second iguana (not the digging individual, which was in the grass to the right of the apron at the time).

Finally, we re-set cameras from 9–16 November 2021 at the same burrow described in detail above, which was also the only burrow where we photographed both tortoises and iguanas in winter or spring 2020–2021 (originally observed 12–15 April 2021). We documented continued burrow sharing between at least two different iguanas (one male, one female, neither one photographed in spring 2020) and one tortoise, with no evidence of burrow abandonment by the tortoise or extensive burrow modification by the iguanas after 7 months. These additional images are not included in any of the above analyses, summaries, or figures.

DISCUSSION

Only 5 out of 69 burrows showed any signs of iguana use, and only one of these five appeared to be in continuous, regular use by iguanas. We observed up to 5 different individual iguanas (never more than 3 at a time) and at least one gopher tortoise actively using the same burrow over a span of 7 months, with some attempts being made by the iguanas to modify the burrow. We did not observe any direct agonistic interactions and did not document displacement of tortoises from their burrows. In our sample, tortoise burrow size, orientation, and canopy coverage varied but did not appear to influence use by iguanas.

The five burrows used by iguanas were mostly above-average in size, but there was not a significant difference between burrows used by iguanas and those not used by iguanas. The higher difficulty of detecting both small burrows and small iguanas probably undermines any strong conclusions about burrow size. Hengstebeck (2018) found that Burmese python presence within tortoise burrows was negatively correlated with burrow entrance width and documented burrow abandonment by tortoises when pythons nested therein.

We found that all tortoise burrows, especially those used by iguanas, were located in very open canopy areas. Even though our site is very open (median canopy cover at random points = 7.1%), tortoises appear to select burrow locations with a canopy that is more open than average (median tortoise burrow canopy cover = 1.3%), which aligns with the microhabitat preferences of iguanas in their native range (Burger and Gochfeld 1991; Fig. 3). Our use of reconnaissance-style surveys might have led us to overlook burrows with dense understory cover, which could have biased our dataset toward burrows in open-canopy areas. This might affect the results if iguanas prefer to use burrows with closed canopies, but based on previous studies of iguana habitat preference, this is not expected to be the case (Burger and Gochfeld 1991; Fig. 3). In contrast, Hengstebeck (2018) found that Burmese python presence within burrows was positively correlated with canopy cover.

Tortoises do not appear to select specific orientations, and many tortoise burrows, especially those that faced north, were located in areas with relatively high canopy coverage. However, subtle trends in orientation can be difficult to detect without very large sample sizes, such as large-scale topographic changes that could influence tortoises to orient their burrows in a common direction (McCoy et al. 1993). We expected burrows with a more open canopy to face north or northeast to maximize cooling and that burrows with a more closed canopy would face south or southwest to maximize solar exposure and temperature throughout the day, but we did not find this to be the case (Fig. 4). It might be that tortoises at this study site, which is located near the southern edge of the range of gopher tortoises, are choosing areas that get more shade throughout the day, which could make their burrows less suitable for invasion by iguanas.

A project that ran concurrent to ours showed that radio-telemetered iguanas ($n = 4$) exhibited high site fidelity to the anthropogenic structures where they were captured over nine months. The four iguanas monitored over this time period were never recorded to use or be around tortoise burrows using radio-telemetry (M. Morningstar, Florida Gulf Coast University, unpubl. data), although one was captured digging at the most active burrow by one of our cameras. Because iguanas also used structures of human origin at our study site, their use of tortoise burrows and thus the potential for tortoise–iguana interactions might be reduced relative to other areas.

Our findings agree with those of Engeman et al. (2009), who suggested that some low level of burrow sharing may be tolerated by tortoises, but that they might be repelled from burrows at high levels of iguana use (≥ 4 iguanas/burrow). We never documented >3 iguanas concurrently using a single burrow, although we documented at least 5

individual iguanas using the same burrow (also occupied by a tortoise) over a span of at least 7 months. Because the iguana population at this site is still small and there appears to be ample shelter, iguanas might make more transient use of tortoise burrows, decreasing the intensity of use at any one burrow.

The primary limitation of our study is our small sample of burrows being used by iguanas. This prevented our comparison of burrow characteristics from being balanced and limited our opportunities to directly observe iguana–tortoise interactions. Our surveys were probably of too short a duration to detect burrow abandonment if and when it occurs. Our use of reconnaissance-style surveys might have led us to overlook burrows that were in very dense vegetation. We also could not set trail cameras at every burrow or for more than 4 days at a single burrow, resulting in temporal heterogeneity in opportunity to record iguana–tortoise interactions.

Not every non-native species has detrimental impacts. For example, armadillos occasionally consume tortoise eggs (Douglass and Winegarner 1977, Smith et al. 2012) or modify tortoise burrows (Hermann et al. 2002, Goodman et al. 2018), but it seems that neither behavior occurs at a high frequency and thus armadillos are generally not considered to be a threat to tortoises (Degroote and Ober 2013). Native species, such as Florida mice (*Peromyscus floridanus*), also make structural modifications to tortoise burrows (Jones and Franz 1990). It might be that iguanas, which are more herbivorous than armadillos, are not a major direct threat to tortoises, though they are larger and might reach higher population densities than native commensal rodents. However, two-species occupancy models support the hypothesis that gopher tortoises are excluded from their burrows by black spiny-tailed iguanas (McKnight et al. 2022). Other studies using cameras failed to detect direct interactions but continue to urge caution (Melanson 2021). Indirect ways that iguanas might harm tortoises or their habitat include feeding on the same native plants as gopher tortoises (Krysko et al. 2009) and dispersing the seeds of non-native Brazilian pepper (*Schinus terebinthifolius*; Jackson and Jackson 2007), which could shade food plants or burrow sites and render tortoise habitat unsuitable long-term.

Whether iguanas are a threat to gopher tortoise populations remains a question that requires further research, but at Florida Gulf Coast University’s Buckingham Complex, the two species have co-existed for at least 13 years and possibly up to 32 years. Although we found no evidence of a direct threat to tortoises from iguanas in this population, future research should monitor iguana population growth and should include year-round trail camera surveillance of burrows, concentrating on recording how long and under what circumstances

tortoises and different numbers of iguanas can occupy a single burrow before displacement of the tortoise, and compare the fates of any displaced tortoises to undisturbed conspecifics.

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LITERATURE CITED

- ABRAHAMSON, W. G., AND D. C. HARTNETT. 1990. Pine flatwoods and dry prairies. Pages 103–149 in R. L. Myers and J. J. Ewel, editors. *Ecosystems of Florida*. University of Central Florida Press, Orlando.
- ASHTON, R. E., AND P. S. ASHTON. 2008. *The Natural History and Management of the Gopher Tortoise *Gopherus polyphemus* (Daudin)*. Krieger Publishing Company, Malabar, Florida.
- AVERY, M. L., E. A. TILLMAN, AND K. L. KRYSKO. 2009. *Gopherus polyphemus* (gopher tortoise), *Ctenosaura similis* (Gray's spiny-tailed iguana). Predation. *Herpetological Review* 40:435.
- AVERY, M. L., E. A. TILLMAN, C. SPURFELD, R. M. ENGEMAN, K. P. MACIEJEWSKI, J. D. BROWN, AND E. A. FETZER. 2014. Invasive black spiny-tailed iguanas (*Ctenosaura similis*) on Gasparilla Island, Florida, USA. *Integrative Zoology* 9:590–597.
- BARTOSZEK, I. A., P. T. ANDREADIS, C. PROKOP-ERVIN, G. CURRY, AND R. N. REED. 2018. *Python bivittatus* (Burmese python) and *Gopherus polyphemus* (gopher tortoise). Habitat use, breeding aggregation, and interspecific interaction. *Herpetological Review* 49:353–354.
- BURGER, J., AND M. GOCHFELD. 1991. Burrow site selection by black iguana (*Ctenosaura similis*) at Palo Verde, Costa Rica. *Journal of Herpetology* 25:430–435.
- CRONIN, D. T., C. RIACO, J. M. LINDER, R. A. BERGL, M. K. GONDER, M. P. O'CONNOR, AND G. W. HEARN. 2016. Impact of gun-hunting on monkey species and implications for primate conservation on Bioko Island, Equatorial Guinea. *Biological Conservation* 197:180–189.
- DEGROOTE, L. W., AND H. K. OBER. 2013. An evaluation of the nine-banded armadillo as predators of gopher tortoise and northern bobwhite quail nests in Florida. *American Midland Naturalist* 169:74–85.
- DOUGLASS, J. F., AND C. E. WINEGARNER. 1977. Predators of eggs and young of the gopher tortoise, *Gopherus polyphemus* (Reptilia, Testudines, Testudinidae) in southern Florida. *Journal of Herpetology* 11:236–238.
- DZIADZIO, M. C., AND L. L. SMITH. 2016. Vertebrate use of gopher tortoise burrows and aprons. *Southeastern Naturalist* 15:586–594.
- EDDMAPS. 2023. Early Detection & Distribution Mapping System. The University of Georgia - Center for Invasive Species and Ecosystem Health. <https://www.eddmaps.org/distribution/viewmap.cfm?sub=18182>. Accessed 20 July 2023.

- ENGEMAN, R., E. JACOBSON, M. L. AVERY, AND W. E. MESHAKA JR. 2011. The aggressive invasion of exotic reptiles in Florida with a focus on prominent species: a review. *Current Zoology* 57:599–612.
- ENGEMAN, R. M., B. CONSTANTIN, M. CHRISTIE, AND P. HALL. 2009. *Ctenosaura similis* (black spiny-tailed iguana), *Gopherus polyphemus* (gopher tortoise). Concurrent burrow use. *Herpetological Review* 40:84.
- EPPELSON, D. M., C. R. ALLEN, AND K. F. HOGAN. 2020. Red imported fire ants reduce invertebrate abundance, richness, and diversity in gopher tortoise burrows. *Diversity* 13:7.
- EPPELSON, D. M., AND C. D. HEISE. 2003. Nesting and hatchling ecology of gopher tortoises (*Gopherus polyphemus*) in southern Mississippi. *Journal of Herpetology* 37:315–324.
- FITCH, H. S., AND J. HACKFORTH-JONES. 1983. *Ctenosaura similis*. Pages 394–396 in D. H. Janzen, editor. *Costa Rican Natural History*. University of Chicago Press, Chicago, Illinois.
- FITCH, H. S., AND R. W. HENDERSON. 1978. Ecology and exploitation of *Ctenosaura similis*. *The University of Kansas Science Bulletin* 51:483–500.
- GOODMAN, S. J., J. A. SMITH, T. A. GORMAN, AND C. A. HAAS. 2018. Longevity of gopher tortoise burrows in sandy soils. *Southeastern Naturalist* 17:531–540.
- GUYER, C., AND S. HERMANN. 1997. Patterns of size and longevity of gopher tortoise (*Gopherus polyphemus*) burrows: implications for the longleaf pine ecosystem. *Chelonian Conservation and Biology* 2:507–513.
- HENGSTEBECK, K. C. 2018. Burmese python use of gopher tortoise burrows in southwestern Florida. Thesis, University of Florida, Gainesville.
- HERMANN, S. M., C. GUYER, J. HARDIN WADDLE, AND M. GREG NELMS. 2002. Sampling on private property to evaluate population status and effects of land use practices on the gopher tortoise, *Gopherus polyphemus*. *Biological Conservation* 108:289–298.
- HIPPS, A. C. 2019. Vertebrate and invertebrate commensals in gopher tortoise burrows of southeast Florida. Thesis, Florida Atlantic University, Boca Raton.
- JACKSON, J. A., AND B. J. S. JACKSON. 2007. An apparent mutualistic association between invasive exotics: Brazilian pepper (*Schinus terebinthifolius*) and black spiny-tailed iguanas (*Ctenosaura similis*). *Natural Areas Journal* 27:254–257.
- JONES, C. A., AND R. FRANZ. 1990. Use of gopher tortoise burrows by Florida mice (*Peromyscus floridanus*) in Putnam County, Florida. *Florida Field Naturalist* 18:45–51.
- KRYSKO, K. L., K. M. ENGE, AND P. E. MOLER. 2019. *Amphibians and reptiles of Florida*. University of Florida Press, Gainesville.
- KRYSKO, K. L., F. W. KING, K. M. ENGE, AND A. T. REPPAS. 2003. Distribution of the introduced black spiny-tailed iguana (*Ctenosaura similis*) on the southwestern coast of Florida. *Florida Scientist* 66:141–146.
- KRYSKO, K. L., K. W. LARSON, D. DIEP, E. ABELLANA, AND E. R. MCKERCHER. 2009. Diet of the nonindigenous black spiny-tailed iguana, *Ctenosaura similis* (Gray 1831)(Sauria: Iguanidae), in southern Florida. *Florida Scientist* 72:48–58.
- LANDLER, L., G. D. RUXTON, AND E. P. MALKEMPER. 2021. Advice on comparing two independent samples of circular data in biology. *Scientific Reports* 11:20337.
- LIPS, K. R. 1991. Vertebrates associated with tortoise (*Gopherus polyphemus*) burrows in four habitats in south-central Florida. *Journal of Herpetology* 25:477–481.
- LUND, U., C. AGOSTINELLI, H. ARAI, A. GAGLIARDI, E. GARCÍA-PORTUGUÉS, D. GIUNCHI, J.-O. IRISSON, M. POCERNICH, AND F. ROTOLO. 2001. circular: circular statistics. Version 0.4-95. <<https://cran.r-project.org/web/packages/circular/index.html>>
- MCCOY, E. D., H. R. MUSHINSKY, AND D. S. WILSON. 1993. Pattern in the compass orientation of gopher tortoise burrows at different spatial scales. *Global Ecology and Biogeography Letters* 3:33–40.
- MCKERCHER, E. 2001. *Ctenosaura pectinata* (Iguanidae) on Gasparilla Island, Florida: colonization, habitat use, and interactions with *Gopherus polyphemus*. Thesis, University of Florida, Gainesville.

- McKNIGHT, S. L., B. KLUEVER, D. MACKENZIE, M. ACEVEDO, AND S. JOHNSON. 2022. Interspecific interactions between an invasive and an imperiled reptile. ResearchSquare (preprint). <https://doi.org/10.21203/rs.3.rs-2365580/v1>.
- McRAE, W. A., J. L. LANDERS, AND J. A. GARNER. 1981. Movement patterns and home range of the gopher tortoise. *American Midland Naturalist* 106:165–179.
- MELANSON, L. 2021. Investigating vertebrate relationships of the South Florida gopher tortoise: a study of vertebrate species within scrub, pine rockland, coastal hammock and grassland habitats. Thesis, Florida Atlantic University, Boca Raton.
- METZGER, C. J. 2013. *Python molurus bivittatus* (Burmese python) habitat use / occurrence within *Gopherus polyphemus* burrows. *Herpetological Review* 44:333–334.
- MOORE, J. A., A. C. HIPPS, C. REILAND-SMITH, AND L. FREMONT. 2017. *Leiocephalus carinatus* (northern curlytail lizard). Gopher tortoise burrow associate. *Herpetological Review* 48:848.
- MUSHINSKY, H. R., E. D. MCCOY, J. E. BERISH, R. E. ASHTON JR., AND D. S. WILSON. 2006. *Gopherus polyphemus*—gopher tortoise. Pages 350–375 in P. A. Meylan, editor. *Biology and Conservation of Florida Turtles*. Chelonian Research Monographs. Chelonian Research Foundation, Lunenburg, Massachusetts.
- NACCARATO, A. M., J. B. DEJARNETTE, AND P. ALLMAN. 2015. Successful establishment of a non-native species after an apparent single introduction event: investigating ND4 variability in introduced black spiny-tailed iguanas (*Ctenosaura similis*) in southwestern Florida. *Journal of Herpetology* 49:230–236.
- NAKAZAWA, M. 2023. fmsb: functions for medical statistics book with some demographic data. Version 0.7.5. <<https://cran.r-project.org/package=fmsb>>
- NUÑEZ, L. P. 2016. Molecular analyses of three non-indigenous squamate species in Florida: testing various hypotheses regarding species introductions. Thesis, University of Florida, Gainesville.
- R CORE TEAM. 2023. R: a language and environment for statistical computing. Version 4.1.1. <<https://www.R-project.org/>>
- SMITH, L. L., D. A. STEEN, L. M. CONNER, AND J. C. RUTLEDGE. 2012. Effects of predator exclusion on nest and hatchling survival in the gopher tortoise. *Journal of Wildlife Management* 77:352–358.
- TOWNSEND, J. H., K. L. KRYSKO, AND K. M. ENGE. 2003. The identity of spiny-tailed iguanas, *Ctenosaura*, introduced to Florida, USA. *Herpetozoa* 16:67–72.
- TRUGLIO, M. R., H. T. SMITH, AND W. E. MESHAKA JR. 2008. Use of gopher tortoise burrows (*Gopherus polyphemus*) by the exotic green iguana (*Iguana iguana*) in Southern Florida. *Journal of Kansas Herpetology* 25:22–23.
- WALSH, P. D., AND L. J. WHITE. 1999. What it will take to monitor forest elephant populations. *Conservation Biology* 13:1194–1202.
- WICKHAM, H. 2009. ggplot2: elegant graphics for data analysis. Version 3.4.2. <<https://cran.r-project.org/web/packages/ggplot2/index.html>>
- WITZ, B. W., D. S. WILSON, AND M. D. PALMER. 1991. Distribution of *Gopherus polyphemus* and its vertebrate symbionts in three burrow categories. *American Midland Naturalist* 126:152–158.

**ARTHROPODS TAKEN FROM BIRDS ON VACA KEY,
MONROE COUNTY (COLUMBIFORMES: COLUMBIDAE;
PASSERIFORMES: PARULIDAE, STURNIDAE, TURDIDAE)**

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During the week of 2–9 May 2023, four birds were found dead at the same address in the City of Marathon, Vaca Key, Monroe County, Florida. Three of the birds had collided with plate glass windows and the fourth flew into a rotating ceiling fan. As in previous reports, I washed the carcasses as described by Hribar and Miller (2011) and prepared representative slide mounts of any arthropods collected. Also, during that same week, a stray feather was found on the sidewalk next to the same building. I took the feather into the laboratory and examined it under a stereomicroscope. I recorded all mites identified (Table 1) and submitted all arthropod specimens into the Florida State Collection of Arthropods in Gainesville.

I determined that the feather found on the sidewalk was a tail feather from a Mourning Dove (*Zenaida macroura*), after consultation with the United States Fish and Wildlife Service's online photo repository (FWS 2023). I found only one mite; it was a tritonymph and thus difficult to identify, but the general aspect and morphology of the first pair of legs and coxal fields allowed identification as the genus *Falculifer* (Pterolichoidea: Falculiferidae). An unidentified *Falculifer* sp. was reported from Mourning Doves in Alachua and Miami-Dade counties (Conti and Forrester 1981). It is likely that the mite collected and reported herein is *Falculifer isodontus* (Gaud and Barre 1992), which is known from other *Zenaida* species in the Caribbean and from Mourning Doves in Manitoba, Canada (Gaud and Barré 1992, Galloway et al. 2014).

The Common Yellowthroat was harboring *Amerodectes hribari* (Analgoidea: Proctophyllodidae), but also an *Analges* species. Most specimens were females but there was one male. This taxon was not definitively identifiable to species because the male was a homeomorph. Some species of feather mites have males that occur in at least two forms, a homeomorph and a heteromorph; in some cases, the polymorphism of males is continuous and intermedial forms are referred to as the mesomorphs (Atyeo 1984, Hernandez and Mironov

Table 1. Mites collected from birds, Vaca Key, Monroe County, Florida, May 2023.

Host	Date collected		Mites	Number collected
Columbiformes: Columbidae	Mourning Dove <i>Zenaida macroura</i>	3 May 2023	Pterolichoidea: Falculiferidae <i>Falculifer</i> sp.	1
Passeriformes: Parulidae	Common Yellowthroat <i>Geothlypis trichas</i>	9 May 2023	Analgoidea: Analgidae <i>Analg</i> es sp.	12
			Analgoidea: Proctophyllodidae <i>Amerodectes hribari</i>	9
			Analgoidea: Proctophyllodidae <i>Proctophyllodes breviquadratus</i>	50
			Dermanyssosidea: Rhinonyssidae <i>Ptilonyssus</i> sp.	2
Passeriformes: Sturnidae	Common Myna <i>Acridotheres tristis</i>	4 May 2023	Trombidiformes: Tenuipalpidae <i>Raoiella indica</i>	1
			Analgoidea: Analgidae <i>Analg</i> es sp.	1
			Analgoidea: Proctophyllodidae <i>Proctophyllodes hylocichlae</i>	14

2017, Dabert et al. 2021). It is possible that this mite may be related to or even conspecific with *Analges digitatus* which is known from the Blackpoll Warbler (*Setophaga striata*) in Canada (Haller 1882) and the Yellow-rumped Warbler (*Setophaga coronata*) in Manitoba, Canada (Galloway et al. 2014).

The mite fauna infesting Ovenbirds (*Seiurus aurocapilla*) in Monroe County has been investigated before (Hribar 2013, 2022). This Ovenbird was harboring an interesting assembly of ectosymbionts. I collected approximately 50 feather mites, *Proctophyllodes breviquadratus* (Proctophyllodidae) and mounted 17 of them on slides. I also found two nasal mites (Dermanyssoidea: Rhinonyssidae). These are probably *Ptilonyssus sairae*. Castro (1948) and Pence and Casto (1976) reported this mite from a number of Parulidae in Florida, including the Ovenbird. However, Knee et al. (2008) collected *Ptilonyssus japuibensis* (Castro 1948) from 11 species of Parulidae, including the Ovenbird, in Manitoba, Canada. Two previous records for rhinonyssid mites from Monroe County were reported from an Indigo Bunting (Hribar 2014) and Common Yellowthroat (Hribar 2020). I collected one red palm mite (*Raoiella indica*; Tetranychoidae: Tenuipalpidae) from the plumage of the Ovenbird. Tenuipalpidae are plant-feeding mites and the red palm mite is an invasive pest of palms and other plants. This mite is native to India and has dispersed to many regions including the Western Hemisphere where it is known from several counties in Florida, including Monroe (Roda et al. 2008). There appear to be few reports of tenuipalpid mites being associated with birds. Ardeshtir (2010) recovered tenuipalpid mites, *Cenopalpus* sp., from bird nests in Iran. Hribar (2014) collected a specimen of *Brevipalpus* sp. from an Indigo Bunting on Vaca Key, Florida.

The Ovenbird also was harboring two other arthropods. I collected one collembolan, *Seira dowlingi* (Entomobryidae). Collembola have been reported previously from birds in Florida; *S. dowlingi* was previously collected from the Northern Mockingbird (*Mimus polyglottos*; Hribar 2021), and another entomobryid species, *Seira brasiliensis* was taken from the Yellow-billed Cuckoo, (*Coccyzus americanus*; Hribar 2023a). Dispersal of Collembola by birds is known to be one way species move to new areas (Christiansen and Bellinger 1994, Lebedeva and Krivolutsky 2003). I also found one biting midge, *Culicoides* sp. (Diptera: Ceratopogonidae). The specimen was too badly damaged to identify beyond genus. This is not a surprising find, as many *Culicoides* species feed facultatively or obligately on birds (e.g., Garvin and Greiner 2003).

The Common Myna (*Acridotheres tristis*) has been called one of the most harmful invasive bird species (Lowe et al. 2000). This bird was first reported in Florida in 2008 (Pranty 2008) and it soon became established in

the state (Kratte 2010). The mite recovered from this bird is a tritonymph and thus not identifiable to species, but it may be *Analges allourus*, the only analgid mite known from the Common Myna. The dorsal shield and setation are comparable to those illustrated by Gaud (1977).

The thrush (*Catharus* sp.) was not identifiable to species. Thrushes are notoriously difficult to identify (Patten 1997). Ouellet (1993) and Frey et al. (2008) used morphometric data to distinguish Bicknell's Thrush (*Catharus bicknelli*) from the Gray-cheeked Thrush (*Catharus minimus*). With the assistance of Heidi Murray I attempted to gather the necessary measurements and perform the calculations, but the results were ambiguous. Frey et al. (2008) even state that their formula will separate most but not all specimens. Ouellet (1993) uses shades of color as characteristics to separate the two species, but color perception is subjective and not all observers see the same shades of colors (Neitz and Jacobs 1990, Jain et al. 2010). Moreover, Ouellet (1993) writes that the best way to distinguish the two species is via their call, which is not possible with a dead bird. Knox (1996) suggests that it is very difficult to identify single specimens because of the wide variation in physical characteristics. In light of the foregoing, I limited identification to the generic level, *Catharus*, with the code GCBT (Pyle 1997) written on the microscope slide labels. The mites removed from this bird were all Proctophyllodidae; based on the morphology of the opisthogastric shields and their position relative to the genital arch, the mites appeared to be *Proctophyllodes hylocichlae*, which is known from the Hermit Thrush (*Catharus guttatus*), in Florida, Maine, and Texas, and Swainson's Thrush (*C. ustulatus*), in California, Maine, and Tennessee (Atyeo and Braasch 1966, McClure 1989, Forrester and Spalding 2003). I collected one minute black scavenger fly (Diptera: Scatopsidae) from the thrush. I could not identify the specimen further than family. One previous collection of a scatopsid midge from a bird has been reported for Vaca Key. An unidentified scatopsid was washed from the plumage of a Common Yellowthroat (Hribar 2023b). Minute black scavenger flies are among the least-known groups of flies in North America and biologies of most species are unknown.

Birds harbor a vast assemblage of ectosymbiotic organisms, ranging from obligate parasites to incidental phoretic organisms. In spite of the considerable amount of work done over the years, there still remains much that is unknown about the diversity of ectosymbionts of birds. The present note is a small contribution to closing the remaining knowledge gaps.

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LITERATURE CITED

- ARDESHIR, F. 2010. A preliminary study on mite fauna of bird nests in Iran. *Podoces* 5:112–115.
- ATYEO, W. T. 1984. A new genus of feather mites and a new expression of male polymorphism (Analgoidea: Avenzoariidae). *Journal of the Kansas Entomological Society* 57:437–455.
- ATYEO, W. T., AND N. L. BRAASCH. 1966. The feather mite genus *Proctophyllodes* (Sarcoptiformes: Proctophyllodidae). *Bulletin of the University of Nebraska State Museum* 5:1–354.
- CASTRO, M. P. DE. 1948. Reestruturação genérica da família Rhinonyssidae Vitzthum, 1935 (Acari: Mesostigmata: Gamasides) e descrição de algumas espécies novas. *Arquivos do Instituto Biológico* 18:253–284.
- CHRISTIANSEN, K., AND P. BELLINGER. 1994. Biogeography of Hawaiian Collembola: the simple principles and complex reality. *Oriental Insects* 28:309–351.
- CONTI, J. A., AND D. J. FORRESTER. 1981. Interrelationships of parasites of white-winged doves and mourning doves in Florida. *Journal of Wildlife Diseases* 17:529–536.
- DABERT J., S. V. MIRONOV, AND M. DABERT. 2021. The explosive radiation, intense host-shifts, and long-term failure to diverge in the evolutionary history of the feather mite genus *Analges* (Acariformes: Analgidae) from the European passerines – a molecular approach. *Zoological Journal of the Linnean Society* 195:673–694.
- FORRESTER, D. J., AND M. G. SPALDING. 2003. *Parasites and Diseases of Wild Birds in Florida*. University Press of Florida, Gainesville.
- FREY, S. J. K., C. C. RIMMER, K. P. MCFARLAND, AND S. MENU. 2008. Identification and sex discrimination of Bicknell's Thrushes using morphometric data. *Journal of Field Ornithology* 79:408–430.
- FWS [UNITED STATES FISH AND WILDLIFE SERVICE]. 2023. The Feather Atlas. Flight Feathers of North American Birds. <https://www.fws.gov/lab/featheratlas/idtool.php>. Accessed 8 May 2023.
- GALLOWAY, T. D., H. C. PROCTOR, AND S. V. MIRONOV. 2014. Chewing lice (Insecta: Phthiraptera: Amblycera, Ischnocera) and feather mites (Acari: Astigmatina: Analgoidea, Pterolichoidea): ectosymbionts of grassland birds in Canada. Pages 139–188 in *Arthropods of Canadian Grasslands, Volume 3*. (H. A. Carcámo, and D. J. Giberson, Eds.). Biological Survey of Canada Monograph Series No. 5, Sackville, Canada.
- GARVIN, M. C., AND E. C. GREINER. 2003. Ecology of *Culicoides* (Diptera: Ceratopogonidae) in southcentral Florida and experimental *Culicoides* vectors of the avian hematozoan *Haemoproteus danilewskyi* Kruse. *Journal of Wildlife Diseases* 39:170–178.
- GAUD, J. 1977. La faune terrestre de l'île de Sainte-Hélène. 4.3. Acariens Sarcoptiformes plumicoles parasites d'oiseaux. *Annales du Musée Royal de l'Afrique Centrale, Sciences Zoologiques Series in-8, Zoologie* 220:260–269.
- GAUD, J., AND N. BARRÉ. 1992. Ficuliferidae (Astigmata, Pterolichoidea) parasites des oiseaux columbiformes des Antilles. II: Le genre *Ficulifer*. *Acarologia* 33:367–375.
- HALLER, G. 1882. Zur Kenntniss der Dermaleichiden. *Archiv für Naturgeschichte* 48:47–79.
- HERNANDES, F. A., AND S. V. MIRONOV. 2017. A systematic review of the feather mite genus *Hyperpedaloptes* Dubinin (Acariformes: Alloptidae) from Old World ibises (Pelecaniformes: Threskiornithidae), with descriptions of previously unknown adult morphs. *Systematic and Applied Acarology* 22:1936–1958.

- HRIBAR, L. J. 2013. Ectoparasites taken from an ovenbird, *Seiurus aurocapilla* (Passeriformes: Parulidae), on Vaca Key, Florida. *Florida Field Naturalist* 41:125–127.
- HRIBAR, L. J. 2014. Parasitic mites collected from perching birds (Aves: Passeriformes) on Vaca Key, Florida. *Florida Field Naturalist* 42:119–123.
- HRIBAR, L. J. 2020. Intriguing plumicoles from the Common Yellowthroat (Aves: Passeriformes) on Vaca Key, Florida. *Florida Field Naturalist* 48:102–104.
- HRIBAR, L. J. 2021. Ectosymbionts from a Northern Mockingbird on Vaca Key, Florida. *Florida Field Naturalist* 49:162–164.
- HRIBAR, L. J. 2022. Additional records of ectosymbionts from the Ovenbird (*Seiurus aurocapilla*) on Vaca Key, Florida. *Florida Field Naturalist* 50:14–16.
- HRIBAR, L. J. 2023a. Arthropod associates of a Yellow-billed Cuckoo *Coccyzus americanus* on Vaca Key, Monroe County, Florida, USA. *Biodiversity Observations* 13:95–97.
- HRIBAR, L. J. 2023b. A minute black scavenger fly (Scatopsidae) taken from a Common Yellowthroat (Aves: Passeriformes). *Fly Times* 70:15–16.
- HRIBAR, L. J., AND G. L. MILLER. 2011. Ectoparasites collected from Common Yellowthroats. *Florida Field Naturalist* 39:138–141.
- JAIN, N., P. VERMA, S. MITTAL, S. MITTAL, A. K. SINGH, AND S. MUNJAL. 2010. Gender based alteration in color perception. *Indian Journal of Physiology and Pharmacology* 54:366–370.
- KNEE, W., H. PROCTOR, AND T. GALLOWAY. 2008. Survey of nasal mites (Rhinonyssidae, Ereyneidae, and Turbinoptidae) associated with birds in Alberta and Manitoba, Canada. *Canadian Entomologist* 140:364–379.
- KNOX, A. 1996. Grey-cheeked and Bicknell's Thrushes: taxonomy, identification, and the British and Irish records. *British Birds* 89:1–9.
- KRATTER, A. W. 2010. Eighteenth report of the Florida Ornithological Society Records Committee: 2008. *Florida Field Naturalist* 38:15–31.
- LEBEDEVA, N. V., AND D. A. KRIVOLUTSKY. 2003. Birds spread soil microarthropods to Arctic islands. *Doklady Biological Sciences* 391:329–332.
- LOWE, S., M. BROWNE, S. BOUDJELAS, AND M. DE POORTER. 2000. 100 of the World's Worst Invasive Alien Species A selection from the Global Invasive Species Database. The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), Gland, Switzerland.
- MCCLURE, H. E. 1989. Occurrence of feather mites (Proctophyllodidae) among birds of Ventura County lowlands, California. *Journal of Field Ornithology* 60:431–450.
- NEITZ, J., AND G. H. JACOBS. 1990. Polymorphism in normal human color vision and its mechanism. *Vision Research* 30:621–636.
- OUELLET, H. 1993. Bicknell's Thrush: taxonomic status and distribution. *Wilson Bulletin* 105:545–572.
- PATTEN, M. A. 1997. The lessons of *Catharus* thrushes revisited. Pages 139–142 in *The Era of Allan R. Phillips: A Festschrift*. (R. W. Dickerman, Ed.). Horizon Communications, Albuquerque, New Mexico.
- PENCE, D. B., AND S. D. CASTO. 1976. Studies on the variation and morphology of the *Ptilonyssus "sairae"* complex (Acarina: Rhinonyssinae) from North American passeriform birds. *Journal of Medical Entomology* 13:71–95.
- PRANTY, B. 2008. Status and distribution of Common Myna (*Acridotheres tristis*) in Florida. *North American Birds* 61:658–665.
- PYLE, P. 1997. *Identification Guide to North American Birds*. Part 1. State Creek Press. Bolinas, California.
- RODA, A., A. DOWLING, C. WELBOURN, J. PEÑA, J. C. V. RODRIGUES, M. A. HOY, R. OCHOA, R. A. DUNCAN, AND W. DE CHI. 2008. Red palm mite situation in the Caribbean and Florida. *Proceedings of the Caribbean Food Crops Society* 44:80–87.

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WINTER RETURN RATES, PATCH FIDELITY, AND RESPONSE TO PRESCRIBED FIRE FOR GRASSHOPPER AND SAVANNAH SPARROWS IN SOUTHWESTERN FLORIDA

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Abstract.—Grassland birds have the highest rates of population declines and are among the highest priority birds for conservation in North America. Although significant effort has been conducted on the breeding ecology of many grassland birds, there have been limited investigations into wintering ecology. We used systematic mist-netting to conduct a five-year assessment of wintering return rates, patch fidelity, and response to prescribed fire for Grasshopper and Savannah Sparrows on grasslands in the Corkscrew Regional Ecosystem Watershed of southwest Florida. Mean annual apparent return rate was 23.9% for Grasshopper Sparrow and 16.1% for Savannah Sparrow, but the addition of gap-year birds (not captured in one year but captured in the following year) increased those rates to 27.7% for Grasshopper Sparrow and 17.4% for Savannah Sparrow. Patch fidelity (returning to the same net lane from the previous capture) was 73.4% between-season for Grasshopper Sparrow and 17.1% for Savannah Sparrow. Within-season patch fidelity was 69.3% for Grasshopper Sparrow and 38.7% for Savannah Sparrow. The differences between species were significant for both between-season and within-season fidelity rates. Grasshopper Sparrow capture rates were significantly higher in years one and two post-fire, but not in year three post-fire when they were similar to the pre-fire levels. The pattern of post-fire capture rates for Savannah Sparrow was similar, but the return to pre-fire levels occurred in year two post-fire. The top performing model for both Grasshopper and Savannah Sparrows was the model that included both the management unit and whether

the unit was burned. The number of unique captures post-fire was significantly more for Grasshopper Sparrow (48.4%) and Savannah Sparrow (91.1%) than pre-fire. Given the continental concern for Grasshopper Sparrow and the continual loss of grassland habitat nationally and regionally, the CREW Grasslands represents important winter habitat and may be representative of the significance of south Florida to wintering grassland birds.

Key Words: Grasshopper Sparrow, Savannah Sparrow, prescribed fire, site fidelity, winter return rates

Grass-dominated ecosystems were historically the most abundant ecotype in North America, accounting for nearly 50% of the continent's land surface (Conner et al. 2001). Since European settlement, most North American grassland ecosystems have lost >80% of their former range (Samson and Knopf 1994, Noss et al. 1995, Brennan and Kuvlesky 2005). In south-central Florida, it is estimated that less than 2% of the dry prairie remains intact in an unaltered state (Noss et al. 1995). The Florida Natural Areas Inventory ranks this habitat as globally imperiled (FNAI and DNR 1990).

Given the degree of grassland habitat loss, it is not surprising that bird species associated with grasslands are in decline (Sauer et al. 2017). Among all the bird guilds in North America, grassland birds have the highest rates of population decline and are among the highest priority birds for conservation in North America (Brennan and Kuvlesky 2005, Askins et al. 2007, North American Bird Conservation Initiative 2009, Rosenberg et al. 2019).

Effective management of migratory grassland bird populations requires information on factors affecting survival throughout their life cycle (Hostetler et al. 2015, Somershoe 2018, Grand et al. 2019, Renfrew et al. 2019). Significant effort has been conducted on the breeding ecology of many grassland birds (e.g., Perlut and Strong 2011, Fromberger et al. 2020, Bernath-Plaisted et al. 2021). However, the need for increased insight into wintering ecology has been put forth as a major research objective needed to advance grassland bird conservation (Herkert and Knopf 1998, Vickery and Herkert 2001, Brennan and Kuvlesky 2005). Recent efforts have assessed within- or between-season winter site fidelity for migrants (Thatcher et al. 2006, Macias and Panjabi 2013, Strasser and Panjabi 2016, Macías-Duarte et al. 2017) and the response species have to the application of prescribed fire (Aldredge 2000, Bechtoldt 2002, Thatcher et al. 2006, Butler et al. 2009, Korosy et al. 2013).

Among grassland bird species continentally, Grasshopper Sparrows (*Ammodramus savannarum*) have lost 78% of their population since the beginning of the Breeding Bird Survey in 1966 (Berlanga et al. 2010), with a significant continental population decline of 2.49% per year (Sauer et al. 2020). The U. S. Fish and Wildlife Service has identified this sparrow as one of 55 focal species to receive increased attention and conservation action

(Ruth 2014). In Bird Conservation Region 31 (i.e., Florida), it is recognized by Partners in Flight as a Species of Continental Importance (Rosenberg et al. 2016). Grasshopper Sparrow is state listed as a Threatened species in five states, and an Endangered species in four states. Seven of these states are in the northeast where south Florida wintering birds may breed. Lastly, in the Florida State Wildlife Action Plan, migratory and wintering Grasshopper Sparrows of the northern subspecies (*A. s. pratensis*) are considered a Species of Greatest Conservation Need (Florida Fish and Wildlife Conservation Commission [FWC] 2019).

Savannah Sparrow (*Passerculus sandwichensis*) is a widespread and relatively common species that is not a species of conservation concern in Florida or elsewhere, except for some isolated sub-specific populations (Rising 2010). Since the beginning of the Breeding Bird Survey in 1966 it has experienced a continental population decline of 1.11% per year (Sauer et al. 2020). It was included in the analyses because capture rates were sufficient to facilitate comparisons with Grasshopper Sparrow. These comparisons elucidated differences in fidelity and impacts of prescribed fire important to understanding conservation needs and activities.

The initial goal of this project was to provide baseline information on wintering sparrow populations in south Florida to assist state agencies in development of habitat management plans. The objectives evolved over time to include: 1) document the presence and abundance of populations of wintering grassland sparrow species, 2) document between-season return rates and between- and within-season patch fidelity for wintering grassland sparrow species, 3) document the response of wintering grassland sparrow species abundance to prescribed fire, and 4) assess the importance of the site to wintering grassland sparrow species in the context of future management of the site and maintenance of these populations.

METHODS

Study Site.—Our study area was situated within an approximately 255 hectares property within the Corkscrew Regional Ecosystem Watershed (CREW) Management Area near Naples and was purchased by the State of Florida in 2014. Florida Fish and Wildlife Conservation Commission (FWC) co-manages the site with the South Florida Water Management District (SFWMD). The site provides landscape diversity and connectivity between the protected sites of Corkscrew Swamp Sanctuary (National Audubon) and a sub-unit of CREW, Bird Rookery Swamp.

The property includes approximately 100 hectares of open grassland where the study was primarily conducted (CREW Grassland), and a separate grassland of approximately 50 hectares 1.6 kilometers north where concurrent research occurred for two years to assess potential movement between sites. At the time of purchase, the grasslands were being used as cattle pasture with previous land uses including row crops and a sod farm. Cattle were removed in the summer of 2015.

The study sites were dominated by a mix of native and non-native wetland and upland grasses that included bushy bluestem (*Andropogon glomeratus*), smutgrass (*Spo-*

robolus indicus), broom sedge bluestem (*Andropogon virginicus*), switchgrass (*Panicum virgatum*), torpedo grass (*Panicum repens*), and paragrass (*Urochloa mutica*). Other common herbaceous species included dog fennel (*Eupatorium capillifolium*), shrubby false buttonweed (*Spermacoce verticillate*), ragweed (*Ambrosia artemisiifolia*), and large flower Mexican clover (*Richardia grandifolia*). Shrubby invaders included cabbage palm (*Sabal palmetto*), primrose willow (*Ludwigia* spp.), Brazilian pepper (*Schinus terebinthifolius*), and saltbush (*Baccharis* spp.).

Capture, Banding, and Prescribed Fire. — In the pilot year of the project (winter 2016-2017), banding was initiated in late January when permits were approved and continued through late March on an opportunistic basis. In the subsequent four winters, banding was conducted in a systematic manner conceptually similar to a MOSI (Monitoring Overwinter Survival) station (Institute for Bird Populations 2023). This protocol included an array of six net lanes with eight continuous nets/lane totaling approximately 100 meters long. Net lanes 1, 3, and 5 (North Unit) were on one side of a central two-track sand road through the site and net lanes 2, 4, and 6 (South Unit) on the other side (Figure 1). The spacing of net lanes was alternated along the central road, and the distance between nearest net lanes was 100-150 meters. The separation of net lanes by the central road facilitated prescribed burning, which was conducted on 18 June 2018 in the North Unit and on 17 April 2019 in the South Unit.

Capture and banding occurred on six mornings per month during five monthly sessions from November through March to represent the winter period. Two net lanes were open each morning and each net lane was open for two mornings in a session or 10 mornings over the course of the winter season. Nets were open from pre-dawn to approximately 0830-0900 EST (2.0-2.5 hours) when sun or wind significantly reduced capture rates. With the help of staff and volunteers, captures were enhanced using systematic

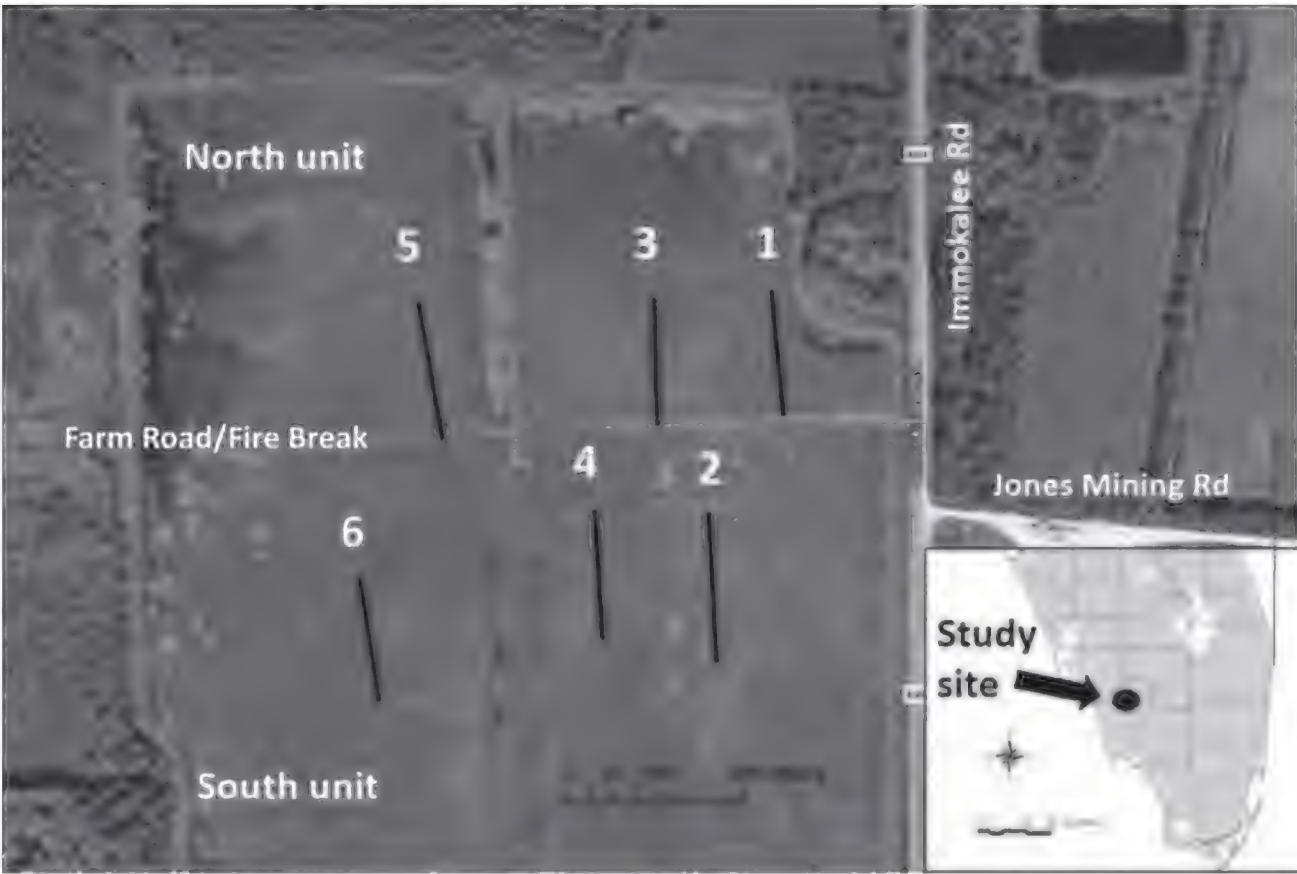


Figure 1. Location of study site, net lanes, and prescribed fire management units for data collected 2017-2021 at the CREW Grassland, Collier County, Florida.

flushing of birds (i.e., flush-netting) towards stationary mist nets using a 75-meter rope. All birds were banded with a USGS aluminum band on the right leg.

Banding at the second grassland was conducted for two winter seasons (2018-2019 and 2019-2020) to assess potential movement of birds between the two sites. There were two net lanes of the same length as the CREW Grassland using the same daily protocol but only during December, January, and February due to other time commitments.

Data Analysis.—Statistical analyses are presented as descriptive summaries of the data (i.e., percents, means) with some inferential interpretation (i.e., Z-test) to assess statistical significance among population means using an alpha value of 0.05. We used the following definitions:

Capture rates of all individuals (i.e., unbanded and previously banded birds) were quantified as the number of birds/net-hour.

Return rate was quantified as the between-season captures measured by 1) the percent of birds recaptured from the banded population in the previous year (i.e., apparent return rate), and 2) the apparent return rate plus “gap-year” birds that were not captured in one season but were captured in a subsequent season (indicating survival during the gap-year and possible fidelity to the site as described herein). The latter could not be estimated for the final season (2020-2021) because gap-year birds did not exist with the cessation of the study.

Patch fidelity was quantified using both between- and within-season captures based on the proportion of individuals captured in the same net lane as the previous capture.

Analyses only included results from the larger CREW Grassland. Data from the smaller grassland were only evaluated to assess the movement of individuals between sites.

We also performed statistical analyses to test whether the number of captures per trap session changed as a response to prescribed fire. We used R statistical software (R Core Team 2023) and established significance at $\alpha = 0.05$. We used a separate generalized linear mixed effect model for Grasshopper Sparrow and Savannah Sparrow with the number of unique individuals captured in a trapping event as the dependent variable (log transformed) with the management unit and whether the trap session was before or after the unit was burned as independent fixed effects. We controlled for uneven sampling effort by using the number of net hours as a random effect. We checked for model assumption of equal mean and variance for Poisson data before model interpretation by testing whether the ratio of the global model’s residuals to its residual degrees of freedom were greater than one. The number of unique captures per day was overdispersed for both Grasshopper ($\chi^2 = 352.79$, ratio = 1.58, $P < 0.01$) and Savannah Sparrows ($\chi^2 = 386.70$, ratio = 1.76, $P < 0.01$), thus we used a negative binomial generalized linear mixed effects model instead (MASS package; Venables and Ripley 2002). We compared all possible models (with and without each fixed effect) using Akaike’s information criterion (corrected for small sample size, AIC_c) and model weight (w). We used a pseudo R^2 using methods developed by Nakagawa and Schielzeth (2013; MuMIn package; Barton 2023) to approximate the amount of variance explained by our top model.

RESULTS

Banding.—We banded 758 sparrows over five winter seasons (Table 1). This included 536 Grasshopper Sparrows and 222 Savannah Sparrows. An additional 53 Grasshopper Sparrows and 28 Savannah Sparrows were banded at the second grassland.

There were annual increases in volunteer effort, but capture effort (i.e., net-hours) and sparrow capture rates did not follow the same

Table 1. Grasshopper and Savannah Sparrow banding by winter season (November-March) at the CREW Grassland, Collier County, Florida, 2017-2021.

Species	CREW Grassland					Totals
	2016-2017 a	2017-2018	2018-2019	2019-2020	2020-2021	
Grasshopper Sparrow	60	83	122	149	122	536
Savannah Sparrow	11	40	62	80	29	222
Totals	71	123	184	229	151	758
Secondary Grassland						
Grasshopper Sparrow			33	20		53
Savannah Sparrow			13	15		28
Totals			46	35		81

^aThere was a reduced time frame (i.e., late January-March) and limited volunteer assistance with mostly passive captures.

pattern (Table 2). Net-hours were highest in 2016-2017 but capture rate was the lowest. Capture rate was highest in 2019-2020 with the third highest net-hours.

Between-Season Return Rates.—Between-year recaptures were recorded for 95 Grasshopper Sparrow and 31 Savannah Sparrow individuals across the four years of sampling recaptures (Table 3). Among Grasshopper Sparrows, one bird had four return years and four birds had three return years. Among Savannah Sparrows, four birds had two return years.

The mean return rate was 23.9% (n = 124) for Grasshopper Sparrow and 16.1% (n = 36) for Savannah Sparrow. These means were not significantly different (P = 0.29). There were multiple gap-year birds each year for Grasshopper Sparrow, but only three gap-year birds total for Savannah Sparrow. These observations increased the mean return rates to 29.5% for Grasshopper Sparrow and 17.4% for Savannah Sparrow.

Annual return rates were similar for Grasshopper Sparrow (range 22.0-30.1%, Figure 2) with no significant difference between the highest and lowest year (P = 0.45). Annual return rates were also similar for Savannah Sparrow (range 18.2-27.2%) except for a drop in 2020-2021 (8.3%). There was no significant difference between the highest and lowest year (P = 0.57), although sample sizes were low.

Patch Fidelity.—Among the 128 between-season return events for Grasshopper Sparrow (95 individuals), the first capture for 73.4% (n = 94) in their return year was in the same net lane from their last capture the previous year(s) (Table 4). Among the 19 examples of gap-year birds, 68.4% (n = 13) returned to the same net lane at least two seasons later, including two double gap-year birds. Among the 35 between-season return events for Savannah Sparrow (31 individuals), the first capture for 17.1% (n = 6) in their return year was in the same net lane

Table 2. Banding effort and Grasshopper and Savannah Sparrow capture rates at the CREW Grassland, Collier County, Florida, 2017-2021.

Season	Mornings	Volunteer Person Days ^a	Net Hours	Sparrows Captured	Sparrow Capture Rate (birds/net hour) ^c
2016-2017	23	^b	284.08	87	0.31
2017-2018	37	49	159.92	235	1.47
2018-2019	31	75	138.90	360	2.59
2019-2020	29	80	148.58	515	3.47
2020-2021	36	98	153.17	290	1.89
Totals	156		884.65	1,487	1.68

^aTotal number of individual days for the season and includes the bander and all volunteers.
^bThere was limited volunteer assistance and mostly passive captures in 2016-2017.
^cIncludes both unbanded (first capture) and recaptures of banded birds.

Table 3. Number of seasons of return events for individual Grasshopper Sparrows and Savannah Sparrows at the CREW Grassland, Collier County, Florida, 2017-2021.

Species	Number Individuals	Number of Seasons Returned				
		1+ ^a	2	2+ ^b	3	4
Grasshopper Sparrow	95	12	17	6	4	1
Savannah Sparrow	31	3	4			

^aBirds with one season of a documented return and one intervening gap-year (i.e., no capture during that year) that likely meant two seasons of returns.

^bBirds with two seasons of documented returns and one intervening gap-year (i.e., no capture during that year) that likely meant three seasons of returns or in two instances birds with one season of a documented return and two intervening gap-years that also likely meant three seasons of returns.

from their last capture the previous year(s) (Table 4). One of the three gap-year birds was captured in the same net lane two seasons later. Among the 335 within-season recapture events (185 individuals) for Grasshopper Sparrow, 69.3% (n = 232) were captured in the same net lane from their previous capture (Table 4). Among the 93 within-season recapture events (66 individuals) for Savannah Sparrow, 38.7% (n = 36) were captured in the same net lane from their previous capture. The differences between species for both between-season and within-season were highly significant ($P = <0.001$).

Prescribed Fire.—The pattern of capture rates by season and prescribed fire management unit were similar for both Grasshopper and Savannah Sparrows (Figure 3). Grasshopper Sparrow capture

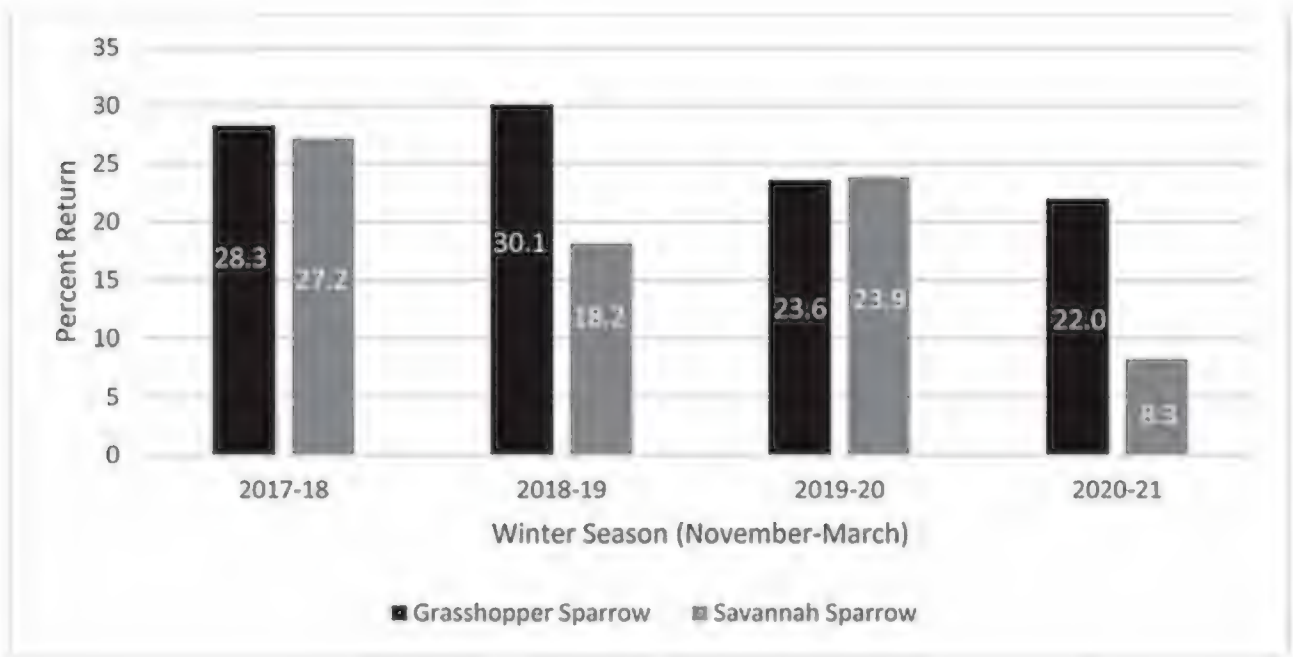


Figure 2. Annual percent return rates for Grasshopper Sparrow and Savannah Sparrow at the CREW Grassland, Collier County, Florida, 2017-2021. There were no significant differences in return rates for either species between the highest and lowest year (all $P > 0.40$).

Table 4. Between-season and within-season recaptures in the same net lane as the previous capture at the CREW Grassland, Collier County, Florida, 2018-2021.

	Between-Season			Within-Season		
	Return Events	Same Net Lane	P value	Recapture Events	Same Net Lane	P value
Grasshopper Sparrow	128	94	< 0.001	335	232	< 0.001
Savannah Sparrow	35	6		93	36	

rates more than doubled in year one post-fire in all net lanes (Figure 4). Capture rates in year two post-fire were lower than year one post-fire but still higher than the pre-fire levels. There were no significant differences in capture rates between net lanes in the pre-fire levels ($P = 0.29$), year one post-fire ($P = 0.15$), or year two post-fire ($P = 0.90$).

Grasshopper Sparrow capture rates in the North Unit were significantly higher in year one post-fire ($P = 0.01$) and year two post-fire ($P = 0.03$), but not in year three post-fire ($P = 0.72$). Capture rates between

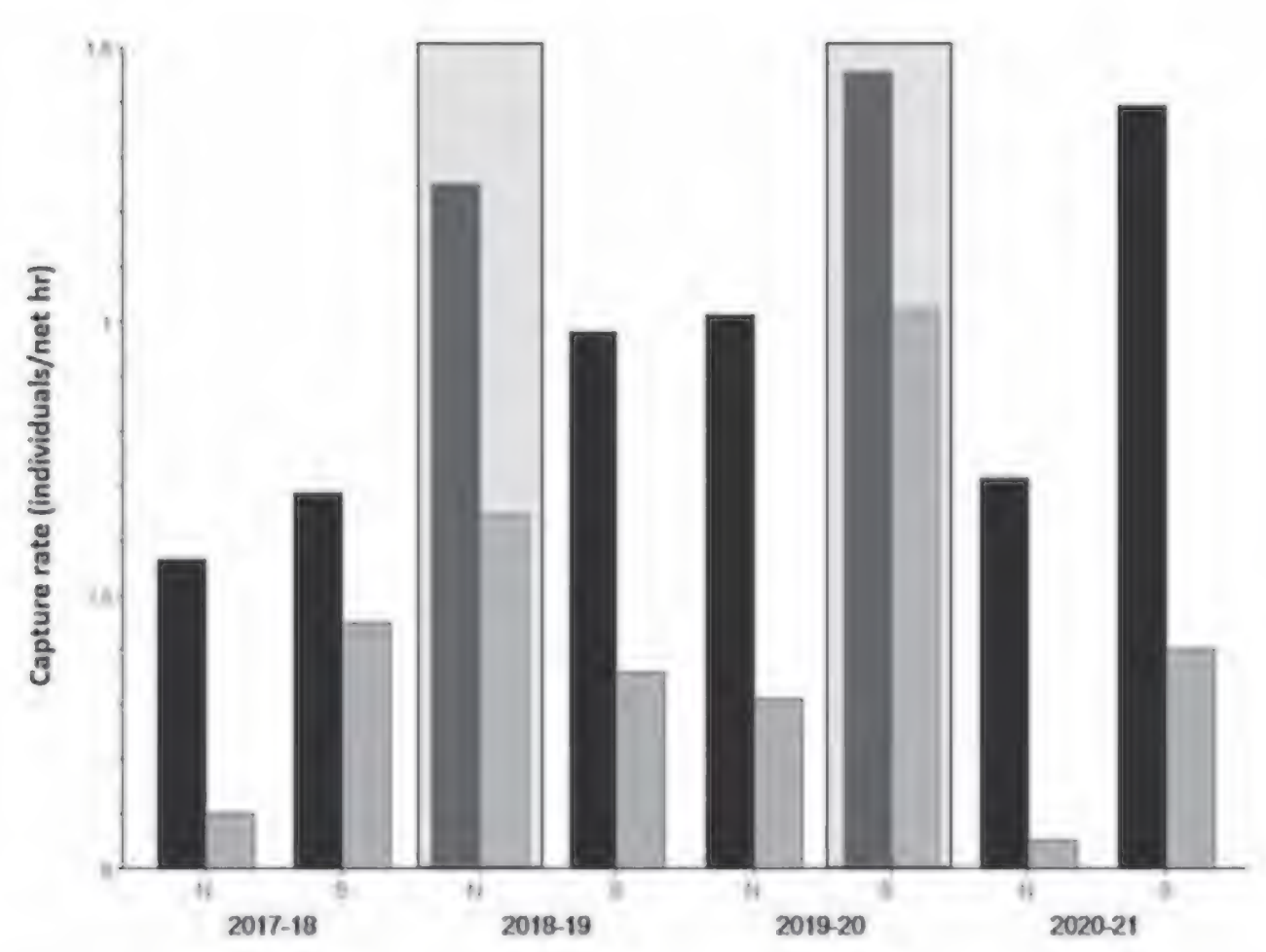


Figure 3. Capture rates (individuals/net hour) of Grasshopper Sparrows (black) and Savannah Sparrows (gray) in either the north (N) or south (S) prescribed fire management unit at the CREW Grassland, Collier County, Florida, 2017-2021. Fire occurred in the season prior to the shaded blocks (i.e., 2018-2019 session on the North Unit and the 2019-2020 session on the South Unit.

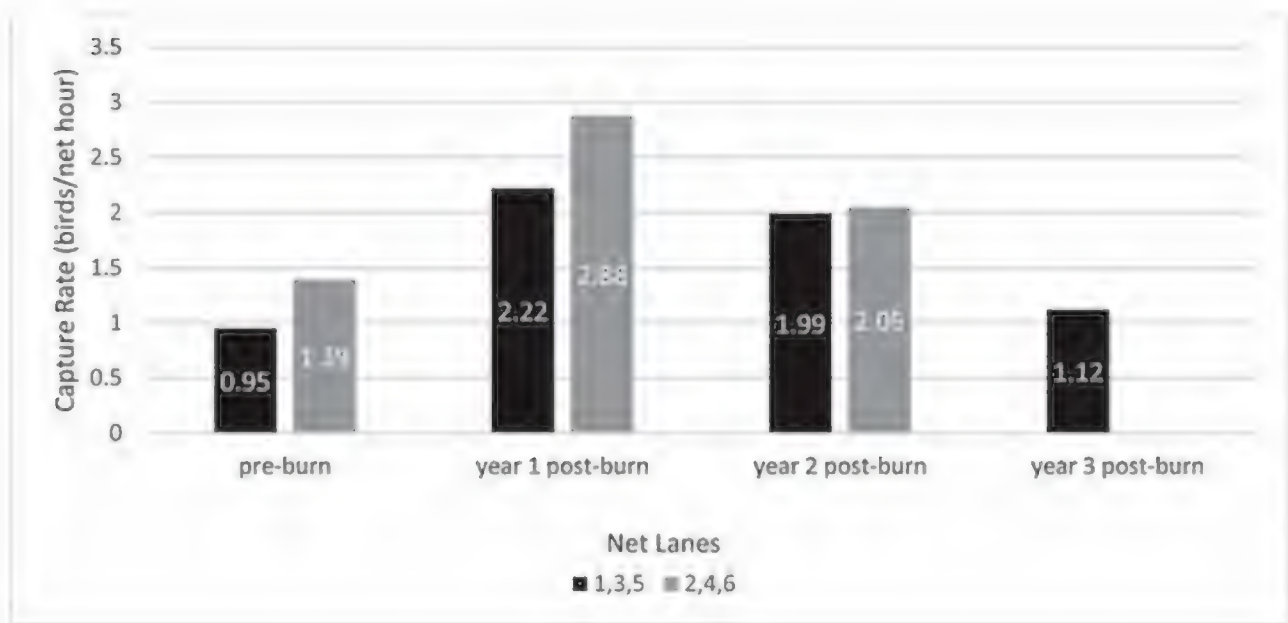


Figure 4. Grasshopper Sparrow capture rates (birds/net-hour) relative to lanes and prescribed fire at the CREW Grassland, Collier County, Florida, 2018-2021. There were no significant differences in capture rates between net lanes in any year (all $P > 0.10$).

years were not significantly different between years one and two post-fire ($P = 0.63$), but nearly significantly higher between years two and three post-fire ($P = 0.07$). Grasshopper Sparrow capture rates in the South Unit were significantly higher in year one post-fire ($P = <0.001$), and nearly significantly higher between years one and two post-fire ($P = 0.07$).

Savannah Sparrow capture rates in year one post-fire in all net lanes were approximately 3-5 times higher than the previous years' pre-fire levels (Figure 5). Capture rates in year two post-fire were more than 50% less than year one post-fire and were similar to the pre-fire levels in the South Unit and greater than double the pre-fire levels in the North Unit. There were no significant differences in capture rates between the net lanes in the pre-fire levels ($P = 0.43$), year one post-fire ($P = 0.16$), or year two post-fire ($P = 0.83$).

Savannah Sparrow capture rates in the North Unit were not significantly different in year one post-fire ($P = 0.15$), between years one and two post-fire ($P = 0.30$), and between years two and three post-fire ($P = 0.51$). There was no significant difference in capture rates between the pre-fire condition and year three post-fire ($P = 0.82$). Savannah Sparrow capture rates in the South Unit were significantly higher in year one post-fire ($P = 0.01$), and between years one and two post-fire ($P = 0.02$).

Among the 26 returns of Grasshopper Sparrow to a different net lane in the three seasons after prescribed fire (i.e., 2018-2021), 57.7% ($n = 15$) returned to a net lane of the same treatment condition (i.e., burned versus unburned) as their last capture. The difference was not significant ($P = 0.45$). Among the 27 returns of Savannah

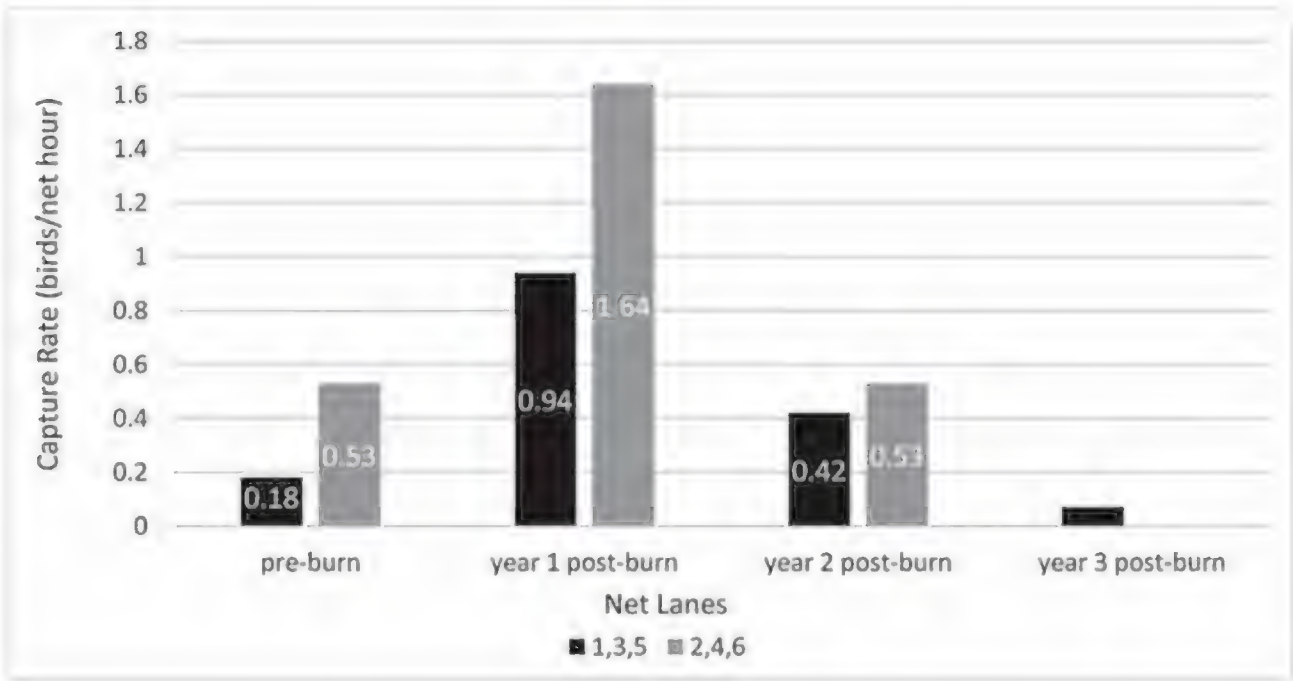


Figure 5. Savannah Sparrow capture rates (birds/net-hour) relative to net lanes and prescribed fire at the CREW Grassland, Collier County, Florida, 2018-2021. There were no significant differences in capture rates between net lanes in any year (all $P > 0.10$).

Sparrow to a different net lane in the three seasons after prescribed fire (i.e., 2018-2021), 33.3% ($n = 9$) returned to a net lane of the same treatment condition (i.e., burned versus unburned) as their last capture. The difference was not significant ($P = 0.25$).

Capture rates in unburned net lanes in the season after a prescribed fire were similar to the previous season for both Grasshopper and Savannah Sparrow except for a reduction of greater than 50% for Savannah Sparrow in the North Unit (Table 5). However, there were no significant differences among any of the four comparisons between species and years (P range = 0.31 - 0.97).

The top performing model for Grasshopper Sparrows ($\Delta AIC_c = 0$, $w = 0.95$, Table 6) was the model that included both the management unit and whether the unit was burned (marginal $R^2 = 0.06$, conditional $R^2 = 0.34$). The number of unique Grasshopper Sparrows captured per trapping event post-fire was significantly more (48.4% greater, 95% CI: 15.8-90.2%, $P < 0.01$) than pre-fire and was significantly more (39.5% greater, 95% CI: 12.5-73.1%, $P < 0.01$) in the South Unit than the North Unit. Similarly, the best performing model for Savannah Sparrows was the one including both the management unit and whether the unit was burned as fixed effects ($\Delta AIC_c = 0$, $w = 0.86$, marginal $R^2 = 0.08$, conditional $R^2 = 0.14$). The number of Savannah Sparrows caught per trap event post-fire was significantly more (91.06% greater, 95% CI: 12.87-220.21%, $P = 0.02$) than pre-fire and significantly more in the South Unit (140.21% greater, 95% CI: 49.52-287.45%, $P < 0.01$).

Table 5. Capture rates (birds/net-hour) in unburned net lanes the seasons before and after a prescribed fire at the CREW Grassland, Collier County, Florida, 2017-2021.

	Net Lanes 2, 4, 6 (North Unit)			Net Lanes 1, 3, 5 (South Unit)		
	2017-2018	2018-2019	P value	2018-2019	2019-2020	P value
Grasshopper Sparrow	1.28 (103)	1.51 (105)	0.63	2.22 (154)	1.99 (148)	0.63
Savannah Sparrow	0.54 (43)	0.52 (36)	0.97	0.94 (65)	0.42 (31)	0.31

Table 6. Model selection for Grasshopper Sparrow and Savannah Sparrow for the number of unique captures per trap event (negative binomial generalized linear mixed effects model) at the CREW Grassland, Collier County, Florida, 2017-2021. Management unit (MU) and if the unit was burned (burn) were dependent variables with net hours as a random effect in all models. The global model includes both dependent variables. Additionally, a null model was run for comparison (null). Models are reported with number of parameters (K), log-likelihood (LL), Akaike’s information criterion corrected for small sample size (AICc) and model weight (*w*).

Species	Model	K	logLik	AICc	ΔAICc	<i>w</i>
Grasshopper Sparrow	global	5	-463.23	936.83	0.00	0.95
	burn	4	-467.89	943.96	7.12	0.03
	MU	4	-468.13	944.44	7.61	0.02
	null	3	-471.06	948.23	11.40	0.00
Savannah Sparrow	global	5	-303.29	616.85	0.00	0.86
	MU	4	-306.18	620.53	3.68	0.14
	null	3	-310.63	627.36	10.52	0.00
	burn	4	-309.85	627.88	11.03	0.00

DISCUSSION

Effort and Protocol.—Annual increases in volunteer assistance for flush-netting likely enhanced efficiency over time due to increased effort. However, the relationship between volunteer effort and sparrow capture rates was not strong. The year with the most volunteer effort only had the third highest sparrow capture rate, and the year with the least volunteer effort had the second highest sparrow capture rate.

The annual occurrence of multiple gap-year birds suggests that some birds were present but not captured during a wintering season. This assumes those gap-year birds were not at other sites, which is likely considering their high site and patch fidelity, and the near absence of movement of birds between the two grasslands. The consequences of our level of sampling the population and the annual presence of multiple gap-year birds suggest that our estimates of annual percentages for return rates are minimum values.

Our modified protocol from the MOSI program was necessary because of that program’s requirement for passive effort (i.e., no attempts to enhance capture rates artificially). Passive effort would have resulted in much lower capture rates in a grassland habitat as experienced during the 2016-2017 season. Our approach of consistent effort on days and net-hours with the use of volunteers and flush-netting is consistent with the active flush-netting of wintering grassland sparrows elsewhere in Florida (Korosy et al. 2013). Resulting enhanced

capture rates made the effort worthwhile for volunteers and increased the amount of data that could be collected and analyzed.

Return Rates.—There are limited data on between-season winter return rates for grassland sparrows, especially Grasshopper Sparrow. However, our return rates for Grasshopper Sparrow and to a lesser extent Savannah Sparrow are higher than reported in other studies. Return rates for wintering Grasshopper Sparrows over five years in the Chihuahua desert of Mexico were 4.1% using the flush-netting methodology (E. Strasser pers. comm.). In north Florida, return rates of Savannah Sparrows were 4% and 8% in consecutive years (Homann 1979), and in Maryland they were 2.6% over a 15-year period (Gimpel et al. 2014). Odum and Hight (1957) reported return rates of Savannah Sparrows at 5.4% to 16.8% using flush-netting over three winters in South Carolina.

Patch Fidelity.—Grasshopper Sparrows at the CREW Grasslands exhibit “serial residency” (Cresswell 2014) by returning to the same sites, and more specifically the same patches within those sites. Even when Grasshopper Sparrow recaptures were not in the same net lane, they were almost always captured only one net lane away, an average distance of approximately 125 meters and potentially within the extent of a winter territory. This degree of patch fidelity enhances likelihood of survival through knowledge of local food resources and predator avoidance (Gauthreaux 1982).

Our patch fidelity results suggest a high degree of winter season fidelity for Grasshopper Sparrow but much less for Savannah Sparrow. This was further supported by the absence of Grasshopper Sparrow movement between the two sites and only one example of Savannah Sparrow movement. In the Chihuahua desert in Mexico, the majority of Grasshopper Sparrows (56-70%) maintained territories throughout the winter with a mean home range of approximately four hectares (Strasser and Panjabi 2016). In Arizona, wintering Grasshopper Sparrows were highly sedentary and remained within defined home ranges, while Savannah Sparrows were variable in residency among sites and moved greater distances when not resident (Gordon 2020a).

Prescribed Fire.—The pattern of post-fire capture rates for Grasshopper Sparrow was consistent among years and burn unit. It was highest in year one post-fire, reduced in year two post-fire, and reduced further in year three post-fire to levels similar to the pre-fire season. The pattern of post-fire capture rates for Savannah Sparrow was also similar among the burn unit and years, but the return to near pre-fire levels occurred in year two post-fire.

While we did see a significant difference in capture rates post-fire, the top model for both Grasshopper Sparrow and Savannah Sparrow did not explain much of the variance in the number of unique captures

(conditional $R^2 = 0.34$ and 0.14 respectively). Because these were the initial prescribed fire events on the study site, it may require multiple seasons of prescribed fire to explain the variance seen in the data. Additional factors not evaluated empirically that may have impacted capture rates include net wariness/avoidance (Marques et al. 2013), vegetation composition especially between prescribed fire management units, and annual variability in predator communities or weather.

The increase in Grasshopper Sparrow and Savannah Sparrow captures in year one post-fire did not appear to be a result of movements of birds from the unburned unit into the burned unit as capture rates in the unburned unit between years were not significantly different. However, most significantly, the new birds that increased the population selected the recently burned habitat over the unburned habitat.

There has been extensive research on Grasshopper Sparrow and Savannah Sparrow response to prescribed fire on the breeding grounds, but limited effort on the wintering grounds. Wintering Grasshopper Sparrow occurrence in central/south Florida was highest year one post-fire (Butler et al. 2009), and in years one and three post-fire (Korosy et al. 2013). In Arizona, wintering Grasshopper Sparrows did not significantly respond to prescribed fire in year one post-fire (Gordon 2000b), and in mesquite grasslands of south Texas, Grasshopper Sparrows declined in abundance in year one post-fire (Reynolds and Krausman 1998).

Wintering Savannah Sparrows in Texas coastal prairie were significantly more abundant in year one post-fire than years two or three post-fire (Baldwin et al. 2007), and density also increased in year one post-fire but declined in years two and three (Marx et al. 2008). Similarly, in grasslands in Arizona, Savannah Sparrow capture rates were higher in year one post-fire but declined in year two post-fire (Gordon 2000b). They also were reported to increase in abundance in year one post-fire in mesquite grasslands of south Texas (Reynolds and Krausman 1998).

Because Grasshopper and Savannah Sparrows are primarily granivorous in winter, they require some exposed soil for foraging (Vickery 1996), which can be provided by regular burning. Prescribed fire may improve winter foraging conditions by reducing dense grass cover at the ground level (Marx et al. 2008), and the increased flowering responses that many plants exhibit following burns also may improve winter food resources (Cox and Jones 2009).

Conservation Significance.—The CREW grasslands likely support a wintering population of approximately 250 Grasshopper Sparrows based on extrapolation of capture rates and the degree of coverage of the grassland with the net array (approximately 60%). This estimate represents a noteworthy stronghold for a species of national and

regional conservation concern in a habitat type that is declining in extent not only in south Florida, but also continentally. The size of this Grasshopper Sparrow population also suggests the potential for other grassland sites to support similarly high densities, and the potential regional importance of grassland habitats as a wintering stronghold of Grasshopper Sparrows in southwest Florida. These results support the suggestion of Butler et al. (2009) that prairies in south Florida are likely a major wintering area for migratory grassland birds.

As the human footprint in Florida expands, important grasslands will continue to decline (Volk et al. 2017). Further loss of this dwindling habitat type will compromise the survival of wintering Grasshopper Sparrows. Winter survival has been suggested as potential major contributor to population declines (Saracco et al. 2010), and conservation of grassland birds in North America must focus on strategies that promote high winter survival (Faaborg et al. 2010a, Saether et al. 1996).

The high proportion of return rates and patch fidelity in Grasshopper Sparrows has strong implications for conservation. On the positive side, these results indicate the adequacy of resources (Hunter et al. 2022) and the presumed high quality of the site for wintering grassland sparrows (Faaborg et al. 2010b). Further, this population can be maintained through the routine management activity of prescribed fire. Our results support the suggestion of Butler et al. (2009) who recommend prescribed fire intervals every two years to maintain suitable habitat for wintering grassland birds in central and south Florida.

On the negative side, the ecological consequences of high dependency on specific wintering areas makes birds more susceptible and less resilient to the loss or alteration of those sites with concomitant negative effects on populations. Forced dispersal from familiar sites increases vulnerability during dispersal and at new sites where there is increased competition with established birds for resources (Cotto et al. 2014). In addition to the loss of grassland habitat, the associated fragmentation of the remaining habitats across the landscape adversely affects sedentary species like Grasshopper Sparrow more than mobile species (Gordon 2000a).

There has been one foreign recovery (bird banded at CREW and recovered elsewhere) of a Grasshopper Sparrow banded in this project. This bird was recovered during the breeding season in northwestern Virginia. These types of records would be of conservation significance if birds are breeding in the many states where they are listed as Threatened or Endangered. There are no other records in the Bird Banding Laboratory of foreign recoveries of Grasshopper Sparrows banded anywhere in Florida or of birds captured in Florida and banded

in another state (D. Bystrak, pers. comm.). However, recent research provides some insight into the migratory connectivity between wintering Grasshopper Sparrows in Florida and their breeding grounds (Hill and Renfrew 2019). Geolocator data from 20 breeding birds in Maryland indicated that most wintered in south Florida, and some passed through south Florida to wintering sites in the Caribbean.

There is a growing body of evidence that suggests overwintering habitat conditions can have a significant impact on an individual migratory birds' reproductive fitness and success on the breeding grounds in the following breeding season (i.e., carryover effects) (e.g., Norris et al. 2004, Webster and Marra 2005, Reudink et al. 2009, Harrison et al. 2011, Marra et al. 2015), including for a grassland bird (Macías-Duarte and Panjabi 2013). Conversely, Blackburn and Cresswell (2016) suggested that overwinter site habitat conditions may have few carryover effects on future survival with a lower level of resources needed compared to breeding birds, and that adequate but familiar sites are more important. Our results of high site and patch fidelity and survival suggest the adequacy of the resources to potentially support enhanced fitness for migration and reproduction.

Given the size of the population of Grasshopper Sparrows at the CREW Grassland, the continental concern for the species, the continuing national and regional loss of grassland habitat, the Threatened or Endangered status in nine northern states where it breeds, and increased recognition of the importance of wintering habitat as part of the full-life cycle, the CREW Grassland likely represents important winter habitat for the conservation of Grasshopper Sparrows and may be representative of the significance of grasslands in south Florida to wintering grassland birds.

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LITERATURE CITED

- ALDREDGE, J. N. 2000. Factors affecting breeding territory size and placement of the Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*). M.S. Thesis, University of Central Florida, Orlando.
- ASKINS, R. A., F. CHÁVEZ-RAMÍREZ, B. C. DALE, C. A. HAAS, J. R. HERKERT, F. L. KNOPF, AND P. D. VICKERY. 2007. Conservation of grassland birds in North America: understanding ecological processes in different regions. *Ornithological Monographs* 64:1–46.
- BALDWIN, H. Q., J. B. GRACE, W. C. BARROW, AND F. C. ROHWER. 2007. Habitat relationships of birds overwintering in a managed coastal prairie. *The Wilson Journal of Ornithology* 119:189–197.

- BARTON, K. 2023. Package ‘MuMIn’ version 1.46.0. Available at [http:// https://cran.r-project.org/web/packages/MuMIn/index.html](http://https://cran.r-project.org/web/packages/MuMIn/index.html).
- BECHTOLDT, C. L. 2002. Habitat use by wintering Henslow’s sparrows (*Ammodramus henslowii*) in relation to fire management. M.S. Thesis, Southeastern Louisiana University, Hammond, LA.
- BERLANGA, H. AND 20 co-authors. 2010. Saving Our Shared Birds: Partners in Flight Tri-National Vision for Landbird Conservation. Cornell Lab of Ornithology: Ithaca, NY.
- BERNATH-PLAISTED, J. S., A. O. PANJABI, N. A. GUIDO, K. D. BELL, N. DRILLING, E. H. STRASSER, S. K. JOHNSON, AND M. D. CORRELL. 2021. Quantifying multiple breeding vital rates in two declining grassland songbirds. *Avian Conservation and Ecology* 16:19.
- BLACKBURN, E. AND W. CRESSWELL. 2016. High winter site fidelity in a long-distance migrant: implications for wintering ecology and survival estimates. *Journal of Ornithology* 157:93–108.
- BRENNAN, L. A., AND W. P. KUVLESKY. 2005. North American grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* 69:1–13.
- BUTLER, A. B., J. A. MARTIN, W. E. PALMER, AND J. P. CARROLL. 2009. Winter use of south Florida dry prairie by two declining grassland passerines. *Condor* 111:511–522.
- CONNER, R., A. SEIDL, L. VANTASSELL, AND N. WILKINS. 2001. United States Grasslands and Related Resources: An Economic and Biological Trends Assessment. Texas A&M Natural Resources Institute.
- COTTO, O., A. KUBISCH, AND O. RONCE. 2014. Optimal life-history strategy differs between philopatric and dispersing individuals in a metapopulation. *American Naturalist* 183:384–393.
- COX, J. A. AND C. D. JONES. 2009. Influence of prescribed fire on winter abundance on Bachman’s Sparrow. *The Wilson Journal of Ornithology* 121:359–365.
- CRESSWELL, W. 2014. Migratory connectivity of Palaearctic–African migratory birds and their responses to environmental change: the serial residency hypothesis. *Ibis* 156:493–510.
- FAABORG, J. AND 19 coauthors. 2010a. Conserving migratory land birds on the North American continent: Do we know enough? *Ecological Applications* 20:398–418.
- FAABORG, J. AND 19 co-authors. 2010b. Recent advances in understanding migration systems of New World land birds. *Ecological Monograph* 80:3–48.
- FLORIDA FISH AND WILDLIFE CONSERVATION COMMISSION. 2019. Florida’s Wildlife Legacy Initiative: Florida’s State Wildlife Action Plan. Tallahassee, Florida.
- FLORIDA NATURAL AREAS INVENTORY (FNAI) AND DEPARTMENT OF NATURAL RESOURCES (DNR). 1990. Guide to the natural communities of Florida.
- FROMBERGER, M. A., A. J. CAMPOMIZZI, Z. M. LEBRUN-SOUTHCOTT, A. L. PINTARIC, N. M. MACDONALD, AND E. NOL. 2020. Factors affecting Bobolink nest survival across grassland types. *Avian Conservation and Ecology* 15:13.
- GAUTHREAUX, S. A., JR. 1982. The ecology and evolution of avian migration systems. Pages 93-167 in D. S. Farner and J. R. King (editors), *Avian Biology*, Volume 6. Academic Press, New York and London.
- GIMPEL, M. E., D. M. SMALL, J. G. GRUBER. 2014. Winter site fidelity of six sparrow species in Maryland. *North American Bird Bander* 39:45–51.
- GORDON, C. E. 2000a. Movement patterns of wintering grassland sparrows in Arizona. *Auk* 117:748–759.
- GORDON, C. E. 2000b. Fire and cattle grazing on wintering sparrows in Arizona grasslands. *Journal of Range Management* 53:384–389.
- GRAND, J., C. WILSEY, J. X. WU, AND N. L. MICHEL. 2019. The future of north American grassland birds: incorporating persistent and emergent threats into full annual cycle conservation priorities. *Conservation Science and Practice* 2019: e20.

- HARRISON, X. A., J. D. BLOUNT, R. INGER, D. R. NORRIS, AND S. BEARHOP. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80:4–18.
- HERKERT, J. R., AND F. KNOPF. 1998. Research needs for grassland bird conservation. Pages 273–282 in J. M. Marzluff, and R. Sallabanks (editors). *Avian Conservation: research and management*. Island Press, Washington, D.C.
- HILL, J. M. AND R. B. RENFREW. 2019. Migratory patterns and connectivity of two North American grassland bird species. *Ecology and Evolution* 9:680–692.
- HOMANN, P. H. 1979. Wintering bird densities in north Florida. *North American Bird Bander* 4: 154–157.
- HOSTETLER, J. A., T. S. SILLETT, AND P. P. MARRA. 2015. Full-annual-cycle population models for migratory birds. *Auk* 132:433–449.
- HUNTER, E. A., A. DWIRE, AND T. M. SCHNEIDER. 2022. Demography and site fidelity of a grassland bird, the Henslow's Sparrow, in powerline right-of-way habitat. *Journal of Field Ornithology* 93:9.
- INSTITUTE FOR BIRD POPULATIONS. 2023. MOSI: Monitoring neotropical migrants in winter. <https://www.birdpop.org/pages/mosi.php>.
- KOROSY, M. G., J. S. REECE, R. F. NOSS. 2013. Winter habitat associations of four grassland sparrows in Florida dry prairie. *The Wilson Journal of Ornithology* 125:502–512.
- MACÍAS-DUARTE, A. AND A. O. PANJABI. 2013. Association of habitat characteristics with winter survival of a declining grassland bird in Chihuahuan Desert grasslands of Mexico. *Auk* 130:141–149.
- MACIAS-DUARTE, A., A. O. PANJABI, E. H. STRASSER, G. J. LEVANDOSKI, I. RUVALCABA-ORTEGA, P. F. DOHERTY, AND C. I. ORTEGA-ROSAS. 2017. Winter survival of North American grassland birds is driven by weather and grassland condition in the Chihuahuan Desert. *Journal of Field Ornithology* 88:374–386.
- MARQUES, J. T., M. J., RAMOS PEREIRA, T. A. MARQUES, C. D. SANTOS, J. SANTANA, P. BEJA, AND J. M. PALMEIRIM. 2013. Optimizing sampling design to deal with mist-net avoidance in Amazonian birds and bats. *PLoS ONE* 8(9): e74505.
- MARRA, P. P., C. E. STUDDS, S. WILSON, T. S. SILLETT, T. W. SHERRY, AND R. T. HOLMES. 2015. Non-breeding season habitat quality mediates the strength of density-dependence for a migratory bird. *Proceedings of the Royal Society of Biological Sciences* 282.
- MARX, D. E., S. J. HEJL, AND G. HERRING. 2008. Wintering grassland bird habitat selection following summer prescribed fire in a Texas Gulf Coast tallgrass prairie. *Fire Ecology* 4:46–62.
- NAKAGAWA S. AND H. SCHIELZETH. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecological Evolution* 4:133–142.
- NORTH AMERICAN BIRD CONSERVATION INITIATIVE, U.S. COMMITTEE, 2009. *The State of the Birds 2009 Report*, United States of America. U.S. Department of the Interior: Washington, D.C.
- NORRIS, D. R., P. P. MARRA, T. K. KYSER, T. W. SHERRY, AND L. M. RATCLIFFE. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of Biological Sciences* 271:59–64.
- NOSS, R. F., E. T. LAROE III, AND J. M. SCOTT. 1995. *Endangered ecosystems of the United States: a preliminary assessment of loss and degradation*. National Biological Service.
- ODUM, E. P. AND G. L. HIGHT. 1957. Use of mist nets in population studies of winter fringillids on the AEC Savannah River area. *Bird Banding* 28:203–213.
- PERLUT, N. G., AND A. M. STRONG. 2011. Grassland birds and rotational-grazing in the northeast: breeding ecology, survival and management opportunities. *Journal of Wildlife Management* 75:715–720.
- R CORE TEAM. 2023. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

- RENFREW, R. B., K. A. PETERS, J. R. HERKERT, K. R. VANBEEK, AND T. WILL. 2019. A full life cycle conservation plan for Bobolink (*Dolichonyx oryzivorus*). U.S. Fish & Wildlife Service.
- REUDINK, M. W., P. P. MARRA, T. K. KYSER, P. T. BOAG, K. M. LANGIN, AND L. M. RATCLIFFE. 2009. Non-breeding season events influence sexual selection in a long-distance migratory bird. *Proceedings of the Royal Society B: Biological Sciences* 276:1619–1626.
- REYNOLDS, M. C. AND P. R. KRAUSMAN. 1998. Effects of winter burning on birds in mesquite grassland. *Wildlife Society Bulletin* 26:867–876.
- RISING, J. D. 2010. The many Savannah Sparrows. *Birding* 42:44–55.
- ROSENBERG, K. V. AND 23 co-authors. 2016. Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States. Partners in Flight Science Committee.
- ROSENBERG, K. V., A. M. DOKTER, P. J. BLANCHER, J. R. SAUER, A. C. SMITH, P. A. SMITH, J. C. STANTON, A. PANJABI, L. HELFT, M. PARR, AND P. P. MARRA. 2019. Decline of the North American avifauna. *Science* 366:120–124.
- RUTH, J. M. 2014. Status Assessment and Conservation Plan for the Grasshopper Sparrow (*Ammodramus savannarum*). Version 1.0. U.S. Fish and Wildlife Service, Lakewood, Colorado. 109 pages.
- SAETHER, B. E., T. H. RINGSBY, AND E. ROSKFT. 1996. Life history variation, population processes, and priorities in species conservation: towards a reunion of research paradigms. *Oikos* 77:217–226.
- SAMSON, F., AND F. KNOFF. 1994. Prairie conservation in North America. *Bioscience* 44.
- SARACCO, J. F., A. ROYLE, D. F. DESANTE, AND B. GARDNER. 2010. Modeling spatial variation in avian survival and residency probabilities. *Ecology* 91:1885–1891.
- SAUER, J. R., W. A. LINK, AND J. E. HINES. 2020. The North American Breeding Bird Survey, Analysis Results 1966–2019: U.S. Geological Survey data release.
- SAUER, J. R., D. K. NIVEN, J. E. HINES, D. J. ZIOLKOWSKI, JR, K. L. PARDIECK, J. E. FALLON, AND W. A. LINK. 2017. The North American Breeding Bird Survey, Results and Analysis 1966–2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, MD.
- STRASSER, E. H. AND A. O. PANJABI. 2016. Identifying limiting factors for grassland birds wintering in the Chihuahuan Desert. Bird Conservancy of the Rockies, Brighton, Colorado. Final Report, submitted to U.S. Forest Service International Program.
- SOMERSHOF, S. G. (EDITOR). 2018. A full annual-cycle conservation strategy for Sprague's Pipit, Chestnut-collared and McCown's Longspurs, and Baird's Sparrow. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C.
- THATCHER, B. S., D. G. KREMENTZ, AND M. S. WOODREY. 2006. Henslow's sparrow winter-survival estimates and response to prescribed burning. *Journal of Wildlife Management* 70:198–206.
- VENABLES, W. N. AND B. D. RIPLEY. 2002. Modern applied statistics with S. 4th edition, Springer, New York.
- VICKERY, P. D. 1996. Grasshopper Sparrow (*Ammodramus savannarum*) in *The Birds of North America*, No. 239 (A. Poole and F. Gill, editors). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.
- VICKERY, P. D., AND J. R. HERKERT. 2001. Recent advances in grassland bird research: where do we go from here? *The Auk* 118:11–15.
- VOLK, M. I., T. S. HOCTOR, B. B. NETTLES, R. HILSENBECK, F. E. PUTZ, AND J. OETTING. 2017. Florida Land Use and Land Cover Change in the Past 100 Years. Pages 51–82 in *Florida's Climate: Changes, Variations, and Impacts*. Florida Climate Institute.
- WEBSTER, M. S. AND P. P. MARRA. 2005. The importance of understanding migratory connectivity and seasonal interactions. Pages 199–209 in *Birds of Two Worlds: The Ecology and Evolution of Migration* (R. Greenberg and P. P. Marra, editors). Johns Hopkins University Press, Baltimore, MD.

INTERACTIONS BETWEEN SYMPATRIC FLORIDA SCRUB-JAYS AND SOUTHEASTERN AMERICAN KESTRELS

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Abstract.—The Florida Scrub-Jay (*Aphelocoma coerulescens*) and the Southeastern American Kestrel (*Falco sparverius paulus*) are imperiled species of conservation concern that occur sympatrically in Florida scrub habitat. Despite their overlap in scrub habitat, little information is available about agonistic encounters between these species. During concurrent bird research projects in Ocala National Forest, we opportunistically noted 18 interactions where the two species came within 10 m of each other. These primarily consisted of one species simply displacing the other from a perch without pursuit, and both species initiated these interactions. We found no evidence that Southeastern American Kestrels pose a threat to Florida Scrub-Jays, especially given their small size relative to the scrub-jay and their predominantly invertebrate diet. More fine-scale observations are needed to understand potential benefits that the species might accrue through their coexistence.

Key words: Florida scrub-jay; scrub; behavior; interspecific interactions; agonism

The Florida Scrub-Jay (*Aphelocoma coerulescens*; hereafter scrub-jay) and Southeastern American Kestrel (*Falco sparverius paulus*; hereafter kestrel) are both imperiled species of conservation concern (USFWS 2007, FWC 2011) that occupy early successional habitats in Florida. *F. s. paulus* is a resident non-migratory subspecies (Ruegg et al. 2021) that is smaller than the migratory *F. s. sparverius* (hereafter migratory kestrel) that winters in Florida (Smallwood and Bird 2002). The scrub-jay is endemic to Florida scrub, a shrubland plant community occurring primarily on nutrient-poor sandy ridges in peninsular Florida (Myers 1990, Florida Natural Areas Inventory 2010), whereas the kestrel uses a broader range of open habitats, including scrub, pasture, prairie, and open pine (*Pinus* spp.) forest (FWC 2011, Miller et al. 2019, Miller et al. 2020). Despite their overlap in scrub habitat, little information is available about agonistic encounters between these species.

The scrub-jay eats primarily arthropods and acorns (Woolfenden and Fitzpatrick 1996) whereas the kestrel preys primarily on arthropods and lizards and occasionally small rodents (Bohall-Wood and Collopy 1987, Bird and Palmer 1988). Within scrub, both species prefer low vegetation containing patches of bare ground (Breininger et al. 1998, Beatty 2019, FWC 2019). Both species also frequently perch at the tops of shrubs and trees either scanning for predators and conspecific intruders or prey on the ground. Some biologists in Florida have expressed concern that promoting kestrels with nest boxes could potentially increase negative interactions with the scrub-jay and other imperiled bird species (K. Miller, personal observation).

During concurrent research studies of scrub-jays and kestrels in Ocala National Forest (hereafter Ocala NF) during 2015, 2018, and 2019, we and our colleagues repeatedly observed the two species occupying the same patches of habitat. We report here on our opportunistic observations of interactions between the species.

METHODS

Study area.—The Ocala NF occurs in Lake, Marion, and Putnam counties in north-central Florida between the Ocklawaha River and St. Johns River. Ocala NF supports the largest remaining breeding populations of both scrub-jays (USFWS 2007, Miller et al. 2023) and kestrels (FWC 2011, Miller et al. 2020). Ocala NF encompasses approximately 91,000 ha of scrub habitat managed for multiple objectives that include forest products, wildlife habitat, and recreation. Early successional habitat for scrub-jays and kestrels occurs in hundreds of small (mostly ≤ 60 ha, but recently larger; Hinchee and Garcia 2017) stands of regenerating scrub embedded within an extensive matrix of young sand pine forest (US Forest Service 2009, Hinchee and Garcia 2017). The effects of forest management on the specific habitat needs of individual bird species at Ocala NF have been studied only recently (e.g., Miller and Shea 2021, Beatty et al. 2022). Florida scrub is a pyrogenic plant community characterized by mostly treeless, open expanses of low shrubs dominated by evergreen, or nearly evergreen, oak (*Quercus* spp.) species, principally myrtle (*Q. myrtifolia*), Chapman's (*Q. chapmanii*), and sand live oak (*Q. geminata*) at Ocala NF (Myers 1990).

Observations.—When the two species were observed occurring <10 m apart, we took field notes on the number of individuals involved, the distance between them, which species perched higher, and whether one displaced or chased the other. For our purposes, we defined a displacement as one individual taking over another's perch without further pursuit. If we observed an agonistic encounter, we noted which bird seemed to be the initiator. Observations were made with or without binoculars when at close range (<30 m) and with binoculars when farther away. Distance estimates between species were crude visual assessments to the nearest meter, which we subsequently grouped into bins of ≤ 1 m, 1-5 m, and 5-10 m. Observations were made during the breeding seasons of 2015, 2018, and 2019, principally April through July, when only resident non-migratory kestrels were on site. In some cases, the subjects of our observation were seen near their nests, which were being monitored as part of other research projects.

RESULTS

We opportunistically observed 18 close interactions between scrub-jays and kestrels in Ocala NF. Ten (55%) interactions were between

one scrub-jay and one kestrel, five (28%) were between two scrub-jays and one kestrel, and three (17%) were between three scrub-jays and one kestrel. In 15 of 18 encounters, the kestrel was initially perched higher than the scrub-jay.

Birds approaching within 1 m of each other nearly always resulted in agonistic behavior (6 of 7 observations; 86%; Fig. 1). The one exception was in early May 2019, when we observed two scrub-jays fly into a pine tree and perch <1 m below a male kestrel that was already present; all individuals remained in the tree peaceably for approximately 2 min before the kestrel flew down to the ground in an unsuccessful hunting attempt and subsequently left the area.

Most agonistic encounters we observed were simply one bird displacing another from a perch without vocalizing or pursuing. Both species initiated these interactions (scrub-jays four times, kestrels six times). On three occasions, we observed a kestrel chase a scrub-jay from the vicinity of a known kestrel nest, but we never observed a kestrel attempt to capture, or even strike, a scrub-jay. Of the 18 close interactions, the most aggressive pursuit involved a scrub-jay observed in mid-May 2018 that closely (within 1 m) pursued a kestrel for >60 m, vocalizing with loud weep calls (Woolfenden and Fitzpatrick 1996) before breaking off the chase.

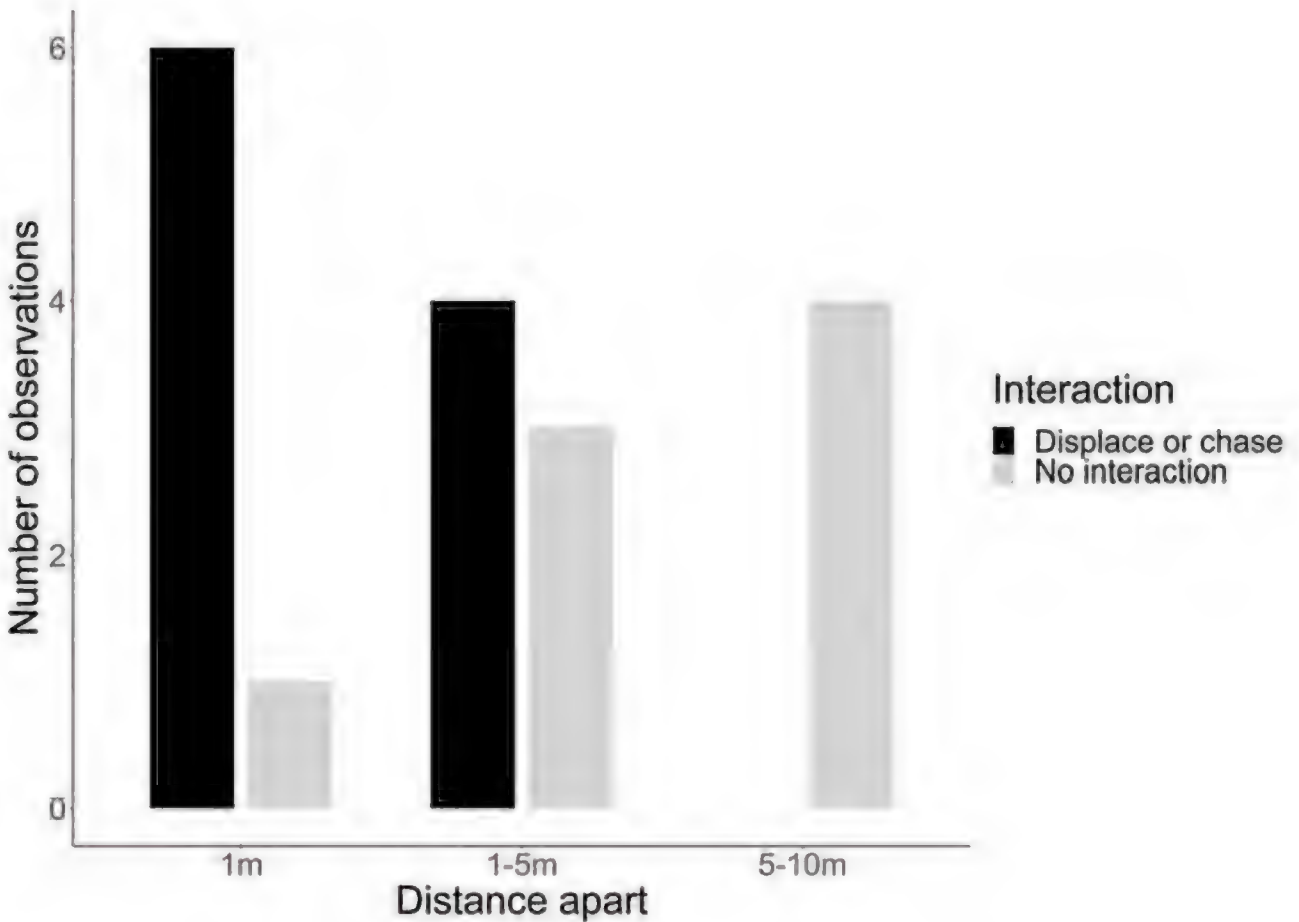


Figure 1. Types of interactions observed between Florida Scrub-Jays and Southeastern American Kestrels, Ocala National Forest, Florida, in years 2015, 2018, and 2019.

DISCUSSION

Florida Scrub-Jays and Southeastern American Kestrels were sympatric in the same patches of scrub at Ocala NF. In a concurrent study, scrub-jays were present in every stand where kestrel nests were found (Beatty 2019, Miller et al. 2020, Beatty et al. 2022). Despite the abundance and proximity of the two species at this site, they rarely interacted and appeared to tolerate each other. When the species were observed in proximity, neither was consistently dominant over the other based on the height of their perches and other factors. We did not observe coordinated scrub-jay behaviors (e.g., warning calls, diving for cover; see McGowan and Woolfenden 1989, Woolfenden and Fitzpatrick 1996) that would indicate they perceived kestrels as a threat.

Despite spending hundreds of hours in these scrub patches, we observed no indication of a predatory impulse by kestrels towards scrub-jays. Migratory kestrels from northern populations are 22-26% heavier than resident Florida kestrels (Layne and Smith 1992) and occasionally consume small birds (typically 0-2% of prey items; Knowlton and Telford 1947, Smith et al. 1972, Balgooyen 1976, Collopy and Koplin 1983; but see Smith and Murphy 1973). When avian prey is taken by migratory kestrels in the United States, it tends to be small, with most species ≤ 40 g (Smith et al. 1972, Collopy and Koplin 1983, Bird and Palmer 1988, Schillaci 2011, McDermot 2016), or no more than 30% of the kestrel's weight (Smallwood and Bird 2002). Florida Scrub-Jays are nearly 80 g (Woolfenden 1978), which is almost as large as resident kestrels (average ~ 100 g; J. Brown and K. Miller, unpublished data). Larger-bodied raptors, especially Cooper's Hawks (*Accipiter cooperii*), Northern Harrier (*Circus cyaneus*), Merlin (*Falco columbarius*), and Great Horned Owl (*Bubo virginianus*), are known predators of nestling, fledgling, and adult scrub-jays (Woolfenden and Fitzpatrick 1996), but those species are several-fold larger than resident kestrels.

An earlier study in north-central Florida found that invertebrates accounted for 96.8% of the diet of resident kestrels, with the remainder primarily lizards (Bohall-Wood and Collopy 1987). Lizards from several genera (including *Anolis*, *Aspidozelis*, *Sceloporus*) are killed by kestrels and brought to nest boxes in north-central Florida (Miller 2017; K. Miller, unpublished data). There is only one record of a bird (reported as "passerine") killed by resident kestrels in Florida (1 of 1,076 prey items; $<0.1\%$; Bohall-Wood and Collopy 1987).

The aggressive encounters that we did observe seemed related, in part, to defending the immediate vicinity around a nest site. Little is known about nonpredatory interspecific interactions of the scrub-jay (Woolfenden and Fitzpatrick 1996), and the potential for mutualism

between these coexisting species should be explored. Predator-mobbing by scrub-jays is known to attract other bird species (McGowan and Woolfenden 1989) and thus may have the potential to alert kestrels to food sources (e.g., snakes). Kestrels are known to drive away larger raptors from their nesting territories (Smallwood and Bird 2002); if kestrel presence discourages or inhibits other avian species from using the same patch of scrub at Ocala NF, then perhaps scrub-jays tolerate kestrels, in part, because they assist in keeping scrub-jay territories safe from intruders.

During hundreds of hours doing bird research in Ocala NF scrub, we and our assistants rarely saw these two species engage in agonistic behavior towards one another. We found no evidence that the kestrel poses a threat to scrub-jay individuals or populations, given their small size relative to the scrub-jay and their predominantly invertebrate diet. More fine-scale observations are needed to understand potential benefits that the species might accrue through coexistence.

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LITERATURE CITED

- BALGOOYEN, T. G. 1976. Behavior and ecology of the American Kestrel (*Falco sparverius* L.) in the Sierra Nevada of California. University of California Publications in Zoology 103:1-83.
- BEATTY, M. A. 2019. Effects of habitat management on Southeastern American Kestrels and other species of conservation concern in Florida scrub. Masters thesis, University of Florida, Gainesville.
- BEATTY M. A., K. E. MILLER, AND R. J. FLETCHER, JR. 2022. Snag density and stand age, but not stand size, explain occupancy and reproduction of an imperiled cavity nester in early successional forest. Avian Conservation and Ecology 17:2.
- BIRD, D. M., AND R. S. PALMER. 1988. American Kestrel. Pages 253–290 in Handbook of North American Birds. Vol. 5: Diurnal Raptors. Part 2 (R. S. Palmer, Ed.), Yale University Press, New Haven, Connecticut.
- BOHALL-WOOD, P. G., AND M. W. COLLOPY. 1987. Foraging behavior of Southeastern American Kestrels in relation to habitat use. Pages 58-65 in The ancestral kestrel. (Bird, D. M., and R. Bowman, Eds). Raptor Research Foundation and MacDonald Raptor Research Centre, Ste. Anne de Bellevue, Quebec.
- BREININGER D. R., V. L. LARSON, B. W. DUNCAN, R. B. SMITH. 1998. Linking habitat suitability to demographic success in Florida scrub-jays. Wildlife Society Bulletin 26:118-128.
- COLLOPY, M. W., AND J. R. KOPLIN. 1983. Diet, capture success, and mode of hunting by female American Kestrels in winter. Condor 85:369–371.
- FLORIDA FISH AND WILDLIFE CONSERVATION COMMISSION [FWC]. 2011. Southeastern American Kestrel Biological Status Review Report. Florida Fish and Wildlife Conservation

- Commission, Tallahassee, FL, USA. <http://myfwc.com/media/2273406/Southeastern-American-Kestrel-BSR.pdf>.
- FLORIDA FISH AND WILDLIFE CONSERVATION COMMISSION [FWC]. 2019. Scrub management guidelines for peninsular Florida. Tallahassee, Florida. <https://myfwc.com/media/19479/scrub-management-guidelines.pdf>
- FLORIDA NATURAL AREAS INVENTORY. 2010. Revised guide to the natural communities of Florida. Tallahassee, Florida.
- HINCHEE, J. K., AND J. O. GARCIA. 2017. Sand pine and Florida Scrub-Jays—An example of integrated adaptive management in a rare ecosystem. *Journal of Forestry* 115:230-237.
- KNOWLTON, G. F., AND P. T. TELFORD. 1947. Insect food of the Eastern Sparrow Hawk in Cache Valley, Utah. *Auk* 64:311.
- LAYNE, J. N., AND D. R. SMITH. 1992. Size comparison of resident and wintering American kestrels in south-central Florida. *Journal of Field Ornithology* 63:256-263.
- MCDERMOT, J. M. 2016. American kestrel (*Falco sparverius*) breeding productivity and diet in a vernal pools and grassland habitat. Dissertation. University of California, Merced.
- MCGOWAN, K. J., AND G. E. WOOLFENDEN. 1989. A sentinel system in the Florida Scrub Jay. *Animal Behaviour* 37:1000-1006.
- MILLER, K. E. 2017. *Aspidoscelis sexlineata sexlineata* (Eastern Six-lined Racerunner) Predation. *Herpetological Review* 48:842-843.
- MILLER, K. E., R. BUTRYN, E. LEONE, AND J. A. MARTIN. 2019. Habitat preferences of nesting southeastern American Kestrels in Florida: the importance of ground cover. *Southeastern Naturalist* 18:192–201.
- MILLER, K. E., M. A. BEATTY, AND R. FLETCHER. 2020. Southeastern American Kestrel data gaps in scrub and sand pine: population estimation, habitat relationships, and management guidelines. Final Report, State Wildlife Grants, Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida.
- MILLER, K. E. AND C. P. SHEA. 2021. Characterizing suitable habitat for the largest remaining population of the threatened Florida scrub-jay *Aphelocoma coerulescens*. *Endangered Species Research* 45:99-107.
- MYERS, R. L. 1990. Scrub and high pine. Pages 150-193 in *Ecosystems of Florida*. (R. L. Myers and J. J. Ewel, Eds.). University of Central Florida Press, Washington, D.C.
- RUEGG, K. C., M. BRINKMEYER, C. M. BOSSU, R. A. BAY, E. C. ANDERSON, C. W. BOAL, R. D. DAWSON, A. ESCHENBAUCH, C. J. MCCLURE, K. E. MILLER, L. MORROW, J. MORROW, M. D. OLEYA, B. RALPH, S. SCHULWITZ, T. SWEM, J-F. THERRIEN, R. VAN BUSKIRK, T. B. SMITH, AND J. A. HEATH. 2021. The American Kestrel (*Falco sparverius*) genoscape: Implications for monitoring, management, and subspecies boundaries. *Ornithology* 138. DOI: 10.1093/auk/ukaa051.
- SCHILLACI, J. 2011. American Kestrel (*Falco sparverius*) attacks Red-cockaded Woodpecker (*Picoides borealis*) fledgling. *Southeastern Naturalist* 10:378-380.
- SMALLWOOD, J. A., AND D. M. BIRD. 2002. American Kestrel (*Falco sparverius*), version 2.0. in *The Birds of North America* (A. F. Poole and F. B. Gill, Eds.). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bna.602>.
- SMITH, D. G., AND J. R. MURPHY. 1973. Breeding ecology of raptors in the eastern Great Basin of Utah. *Brigham Young University Science Bulletin, Biological Series* Vol. 28.
- SMITH, D. G., C. R. WILSON, AND H. H. FROST. 1972. The biology of the American Kestrel in central Utah. *Southwestern Naturalist* 17:73-83.
- U.S. FISH AND WILDLIFE SERVICE (USFWS). 2007. Florida Scrub-Jay (*Aphelocoma coerulescens*) 5-year review: summary and evaluation. USFWS, Jacksonville.
- WOOLFENDEN, G. E. 1978. Growth and survival of young Florida Scrub Jays. *Wilson Bulletin* 90:1-18.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1996. Florida Scrub-Jay (*Aphelocoma coerulescens*), version 2.0. in *The Birds of North America*, No. 228. (A. Poole and F. Gill, Eds.) Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bna.228>.

THE POSSIBLE LOCATION OF MARLOW'S LANDING AND ITS CAROLINA PARAKEET (*Conuropsis Carolinensis*) SPECIMENS

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The Carolina Parakeet (*Conuropsis carolinensis carolinensis*), a brilliant bird of yellow, orange, and green, once filled the swamps and rivers of Florida (McKinley 1985, Snyder 2004). Another subspecies (*C. c. ludovicianus*) lived throughout the Mississippi watershed, east into Ohio and west into Nebraska (Burgio et al. 2017). Although once locally abundant, the species declined quickly during the settlement of the United States and became extinct early in the twentieth century (Burgio et al. 2022). The causes of its extinction remain unresolved.

Six Carolina Parakeet specimens in four different museums bear the location “Marlow’s Landing” or “Marlows” in their collection data. Daniel McKinley knew of five of these specimens but was “unable to trace” the location (1985). Table 1 lists the six parakeet specimens known from Marlows/Marlow’s Landing with collector and date as listed in current catalogs and specimen tags. William K. Lente likely collected all of these specimens in February of 1876. Based on Lente’s collecting history for that month, Marlow’s Landing was likely located in Putnam County, Florida, in the vicinity of Fort Gates.

Discrepancies of collector and year: The date and collector data of the specimen in the Cincinnati Museum Center (CMC: B25362) appears incorrect. The paper catalog at CMC lists the date as 1873 (Rachel Bridgens *in litt.*) and C. E. Aiken as collector. However, McKinley stated that the curator “independently confirmed that the date of 1877 is on the specimen tag” (1985). The current tag on the specimen lists only the collection number (Rachel Bridgens *in litt.*). Whichever year is correct, C. E. Aiken did not collect the specimen. He collected in El Paso County, Colorado in February of 1873 (see University of Colorado Museum of Natural History (UCM) Birds 11384 and 11386) and in January and March of 1877 (see UCM:Birds 12782 and 11633). According to VertNet catalogs (an online database more than 100 museums’ collections - <http://portal.vertnet.org/search>), he did not collect in February 1877 nor ever in Florida. Aiken is not the collector of this specimen.

Table 1. Collection data for six Carolina Parakeet (*Conuropsis carolinensis*) specimens that list Marlow's/Marlow's Landing as a location. Abbreviations as follows: CHAS = Chicago Academy of Science (Peggy Notebaert Nature Museum). USNM = United States National Museum (Smithsonian National Museum of Natural History). CMC = Cincinnati Museum Center. UCM = University of Colorado Museum of Natural History. All were likely collected by William K. Lente.

Museum # (sex)	Collector listed on specimen	Collection date on specimen
CHAS:Bird:15464 (female)	Worthen (McKinley says Lente)	12 February 1876
CHAS:Bird:15468 (male)	Worthen (McKinley says Lente)	12 February 1876
USNM Birds 234976 (female)	Lente	12 February 1876
USNM Birds 234975 (male)	Lente	19 February 1876
CMC: B25362 (male)	C. E. Aiken	12 February 1873 (year?)
UCM:Bird:14505 (male)	Worthen (from Aiken collection)	19 February 1873 (year?)

Worthen also did not collect CMC: B25362 nor UCM:Bird:14505. In fact, with one exception, Worthen likely did not collect any of the 1877 specimens attributed to him. Those include five specimens from February 1877 in Florida, a Great-crested Grebe (*Podiceps cristatus*) from Greenland in April and then a Prothonotary Warbler (*Protonotaria citrea*) from his home in Warsaw, Illinois on 8 May 1877 (SDNHM, USNM, UCM). Such a travel itinerary strains credulity, as does a Greenland expedition that resulted in only one specimen.

Furthermore, Worthen's supposed 1877 specimens closely parallel birds collected by William K. Lente and then sold to E. A. Mearns (see Table 2, last column). Mearns' catalog lists 48 specimens collected by Lente (catalog held at USNM), 6 of them with direct parallels to Worthen specimens. Therefore, Lente likely collected both CMC: B25362 and UCM:Bird:14505, but then sold them to Worthen who sold them to Aiken. It remains unclear when or why the year may have changed on the labels. Lente also probably collected the CHAS specimens, as indicated by the parallel dates.

Lente may have also collected a Carolina Parakeet from Marlow's Landing dated 12 February 1878 (most likely collected in 1876, like the other specimens) that came to the Smithsonian via Worthen (USNM:Birds:78464), for which there is a catalog record but no longer a specimen. A Carolina Parakeet collected at Madina, Florida on 9 February 1877 (UCM:Bird:14504) lists Worthen as collector but is without a parallel to Lente's specimens. The actual collector and the location remain unknown, but the location might be the result of mis-transcribing "Wekiva River;" Wekiva Springs to the river's mouth is entirely within the geo-reference: 28.781684, -81.409062, 11,234 meters of uncertainty (GEOLocate Web Application at www.geo-locate.org).

Location of Marlow's Landing: William Lente's extant specimens and the list from Mearns' catalog (Table 2) allow the partial reconstruction of Lente's movements in February 1876. Lente collected at Marlow's Landing on 12 February 1876 and then at Fort Gates the next day. Lente collected at Fort Gates on 18 February 1876, then in Marlows on 19 February, and then back to Fort Gates on 20 February. Lente collected a male Carolina Parakeet at Fort Gates on 22 February 1876, which was part of Mearns' collection, but the current location of the specimen is unknown. Based on Lente's itinerary, Fort Gates and Marlows were near each other.

Marlow's Landing was possibly the eastern landing point of the Fort Gates Ferry in the 1870s. Fort Gates was founded during the Seminole War (1835-1842), and a ferry crossing the St. John's River from Fort Gates was established in 1853 and continued in use until damaged by a hurricane in 2017. No map from that era displays a

Table 2. William K. Lente’s specimens collected in February 1876, as known from specimens cataloged on VertNet and GBIF and E. A. Mearns’ catalog (at USNM). Carolina Parakeets in bold. Parallels to specimens whose tag indicates Worthen as collector, but with different year, in far-right column. Abbreviations as follows: CMNH = Cleveland Museum of Natural History, RMNH = Rijksmuseum voor Natuurlijke Historie, now Naturalis Biodiversity Center, Leiden, Netherlands (Kamminga and Creuwels 2023).

Species	Date	Locataion	Museum #	sex	Worthen parallel
Ground Dove (<i>Columbina passerina</i>)	2 February 1876	Fort Gates		M	
Ground Dove (<i>Columbina passerina</i>)	2 February 1876	Fort Gates	AMNH Skin-51494(?)	F	
Mourning Dove (<i>Zenaida macroura</i>)	4 February 1876	Fort Gates		M	
Carolina Parakeet (<i>Conuropsis carolinensis</i>)	12 February 1876	Marlow’s Landing	USNM:234976	F	yes; USNM:Birds:78464 (non-extant specimen) lists collection date of 12 February 1878, same location.
Eastern Screech Owl (<i>Megascops asio</i>)	13 February 1876	Fort Gates	AMNH Skin-51686	F	
Loggerhead Shrike (<i>Lanius ludovicianus</i>)	18 February 1876	Fort Gates		M	
American Kestrel (<i>Falco sparverius</i>)	18 February 1876	Fort Gates	AMNH Skin-25341	M	
Carolina Parakeet (<i>Conuropsis carolinensis</i>)	19 February 1876	Marlows	USNM: 234975	M	yes; UCM:Birds:14505 (F) labeled 19 February 1877, same location.
Brown-headed Nuthatch (<i>Sitta pusilla caniceps</i>)	19 February 1876	Marlows	CMNH:Birds:62576 (does not appear in Mearns’ catalog)	U	
Red-cockaded woodpecker (<i>Dryobates borealis</i>)	19 February 1876	Marlows		F	
Yellow-throated Warbler (<i>Dendroica dominica</i>)	20 February 1876	Fort Gates	USNM:235831	M	
Carolina Parakeet (<i>Conuropsis carolinensis</i>)	22 February 1876	Fort Gates		M	
Blue-gray Gnatcatcher (<i>Polioptila caerulea</i>)	24 February 1876	Fort Gates	RMNH.AVES.139409	M	

Table 2. (Continued) William K. Lente’s specimens collected in February 1876, as known from specimens cataloged on VertNet and GBIF and E. A. Mearns’ catalog (at USNM). Carolina Parakeets in bold. Parallels to specimens whose tag indicates Worthen as collector, but with different year, in far-right column. Abbreviations as follows: CMNH = Cleveland Museum of Natural History, RMNH = Rijksmuseum voor Natuurlijke Historie, now Naturalis Biodiversity Center, Leiden, Netherlands (Kamminga and Creuwels 2023).

Species	Date	Locataion	Museum #	sex	Worthen parallel
Common Grackle (<i>Quiscalus quiscula</i>)	24 February 1876	Fort Gates		F	yes; UCM:Birds:13913 (M) labeled 24 February 1877, same location. The bird in Mearns’ catalog may be UCM:Birds:13912
Red-cockaded woodpecker (<i>Dryobates borealis</i>)	25 February 1876	Fort Gates		F	
Florida Scrub-jay (<i>Aphelocoma coerulescens</i>)	25 February 1876	Fort Gates		F	yes, SDNHM:Birds:725 (M) and UCM:Birds9483 (M) labeled 25 February 1877, same location.
Florida Scrub-jay (<i>Aphelocoma coerulescens</i>)	28 February 1876	Fort Gates	USNM:235214	F	

name for the eastern terminus of the ferry. Lente's itinerary during February 1876 makes it clear that Marlow's Landing was likely within a day's journey from Fort Gates, so the location is almost certainly within Putnam County on the St. John's River. Marlow's Landing can be roughly geo-referenced as 29.432388, -81.664498 (GEOLocate Web Application), centered on the site of the most recent eastern terminus of the ferry (See Figure 1). An uncertainty of 10,000 meters seems reasonable to account for a possible day's journey.

Conclusion: William K. Lente collected Carolina Parakeets and other species at Fort Gates, Florida in February of 1876. During that timeframe, he also collected at a place known as Marlow's Landing, which was evidently within a day's journey from Fort



Figure 1. Putnam County, Florida, and its waterways. The approximate location of Marlow's Landing is shown by the star, as described in the text. Circle indicates area of uncertainty. Source: Florida Waterways: Putnam County Outline without Labels, 2008. Florida Center for Instructional Technology, (Tampa, FL: University of South Florida, 2008).

Gates. Lente likely collected all six extant specimens of the Carolina Parakeet labeled as Marlows or Marlow’s Landing in February of 1876. Neither Worthen nor Aiken collected these specimens, despite labels to the contrary. Lente also likely collected two non-extant specimens, one from Fort Gates and one from Marlow’s Landing.

Including the specimens reported here, Putnam County has 13 definite records of the species (Burgio et al. 2018). The St. John’s River, along which these specimens were collected, was a favorite of the species. However, there are relatively few records from north of Lake George, so these specimens offer confirmation of their presence further north on the St. John’s River and relatively late in the decline of the species. While hundreds more specimens would be killed in Florida before 1900, the species was already moving towards extinction by the time Lente collected these specimens. The resolution of the location allows additional data to be added to the comprehensive dataset for the species (Burgio et al. 2018) and, taken as a whole, these data might support new insights into the ecology of the species

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LITERATURE CITED

- AMERICAN MUSEUM OF NATURAL HISTORY. AMNH Bird Collection. http://ipt.vertnet.org:8080/ipt/resource.do?r=amnh_birds (accessed 22 August 2023).
- BURGIO, K. R., C. J. CARLSON, AND M. W. TINGLEY. 2017. Lazarus ecology: Recovering the distribution and migratory patterns of the extinct Carolina parakeet. *Ecology and Evolution* 7: 5467-5475.
- BURGIO, K. R., C. J. CARLSON, AND A. L. BOND. 2018. Georeferenced sighting and specimen occurrence data of the extinct Carolina Parakeet (*Conuropsis carolinensis*) from 1564–1944. *Biodiversity Data Journal*, 6:e25280. doi: 10.3897/BDJ.6.e25280 (accessed 7 September 2023).
- BURGIO, K. R., C. J. CARLSON, A. L. BOND, M. A. RUBEGA, AND M. W. TINGLEY. 2022. The two extinctions of the Carolina Parakeet *Conuropsis carolinensis*. *Bird Conservation International* 32: 498-505.
- CHICAGO ACADEMY OF SCIENCES. CHAS ORNITHOLOGY. [HTTP://IPT.VERTNET.ORG:8080/ipt/resource.do?r=chas_birds](http://IPT.VERTNET.ORG:8080/ipt/resource.do?r=chas_birds) (accessed 22 August 2023).
- CLEVELAND MUSEUM OF NATURAL HISTORY. CMNH BIRDS COLLECTION. [HTTP://IPT.VERTNET.ORG:8080/ipt/resource.do?r=cmnh-birds](http://IPT.VERTNET.ORG:8080/ipt/resource.do?r=cmnh-birds) (accessed 22 August 2023).
- KAMMINGA, P., AND J. CREUWELS. 2023. Naturalis Biodiversity Center (NL) - Aves. Naturalis Biodiversity Center. <https://doi.org/10.15468/dxmzbx> (accessed via GBIF.org on 22 August 2023).

- McKINLEY, D. 1985. The Carolina Parakeet in Florida. FOS Special Publication No. 2. Florida Ornithological Society, Gainesville.
- NATIONAL MUSEUM OF NATURAL HISTORY, SMITHSONIAN INSTITUTION. NMNH Birds. [Http://Collections.Nmnh.Si.Edu/Ipt/Resource?R=Nmnh_extant_dwc-A](http://Collections.Nmnh.Si.Edu/Ipt/Resource?R=Nmnh_extant_dwc-A) (Accessed 22 August 2023).
- SAN DIEGO NATURAL HISTORY MUSEUM. SDNHM BIRDS COLLECTION. http://ipt.vertnet.org:8080/ipt/resource.do?r=sdnhm_birds (accessed 22 August 2023).
- SNYDER, N. F. R. 2004. The Carolina Parakeet: Glimpses of a Vanished Bird. Princeton University Press, Princeton, NJ.
- UNIVERSITY OF COLORADO MUSEUM OF NATURAL HISTORY. UCM BIRDS. http://ipt.vertnet.org:8080/ipt/resource.do?r=ucm_birds (accessed 22 August 2023).

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